Memoirs of the

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# Museum of Victoria

Melbourne Australia
31 December 1994

*Cover:* Devonian limestones on the Broken River, north Queensland; from 'Notes on the Geology of the Colony of Queensland', by Richard Daintree, published in the *Quarterly Journal of the Geological Society of London*, vol. 28 (1872). Daintree carried out the first geological investigations in the Broken River area, located 200 km west of Townsville. The sequence of Palaeozoic rocks, ranging in age from Late Ordovician to Carboniferous, contains a rich fossil fauna, most of which is still poorly documented. Trilobites from Early Silurian siltstones in the lower part of the sequence are described for the first time in this Memoir by David J. Holloway.

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# MEMOIRS

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# MUSEUM OF VICTORIA

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Memoirs of the Museum of Victoria 54(2): 243–269 (1994)

# EARLY SILURIAN TRILOBITES FROM THE BROKEN RIVER AREA, NORTH QUEENSLAND

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**Abstract**

Holloway, D. J., 1994. Early Silurian trilobites from the Broken River area, north Queensland. *Memoirs of the Museum of Victoria* 54: 243–269.

A Late Llandovery (Telychian) trilobite fauna is described from the Poley Cow Formation in the Broken River Province of north Queensland. Taxa recorded are *Kosovopeltis, Proetus* (s.l.), *Warburgella*?, *Otarion, Maurotarion, Scharyia, Youngia, Sphaerexochus, Sphaerocoryphe, Coronocephalus*? aff. *urbis* Strusz, 1980, *Ceratocephala*, the new encrinurid genus *Prostrix*, and the new species *Prostrix amnicola, Batocara fritillum, Gravicalymene*? *vaccina* and *Gaotania bimusa*. *Youngia* and *Gaotania* are recorded from Australia for the first time. *Batocara* Strusz, 1980 is considered to be a senior subjective synonym of *Pacificurus* Ramsköld, 1986a.

Keywords: Trilobita, Early Silurian, Queensland, new taxa.

## Introduction

The Poley Cow Formation (Withnall et al., 1988; Withnall, 1989) is part of the Early Silurian to earliest Devonian Graveyard Creek Group in the Broken River Province (Arnold and Henderson, 1976) of north Queensland. The formation, which consists of up to 550 m of feldspatholithic siltstones, mudstones and polymictic conglomerates, unconformably overlies Ordovician volcanics and clastic sediments of the Judea Formation, and is conformably overlain by limestones and clastic sediments of the Jack Formation (Fielding, 1993). Fossils are not common in the Poley Cow Formation, but a few scattered localities have yielded shelly faunas as well as graptolites and conodonts indicative of a Late Llandovery (Telychian) age (*turriculatus–griestoniensis* and *celloni* Biozones; Jell et al., 1988; Jell and Talent, 1989).

The trilobites described herein were collected from the Poley Cow Formation at Museum of Victoria (NMV) invertebrate fossil locality PL1906 (Fig. 1), situated in the bed of a creek approximately 1.2 km south-east of where the track from Jessey Springs to Wando Vale crosses the Broken River, and approximately 400 m due east of the track (grid reference 703434 on the Burges 1:100,000 sheet 7859). This is the locality reported to yield the richest fauna from the clastic sequence of the Graveyard Creek Group by Jell et al. (1988: 116), who gave a slightly different grid reference, and by Jell and Talent (1989: 200), who marked the locality as S2 on their fig. 144, not S1 as stated in the text. In addition to the trilobites, the fauna from PL1906 also includes brachiopods, bivalves, gastropods, nautiloids, ostracodes and abundant disarticulated crinoid remains, all preserved as

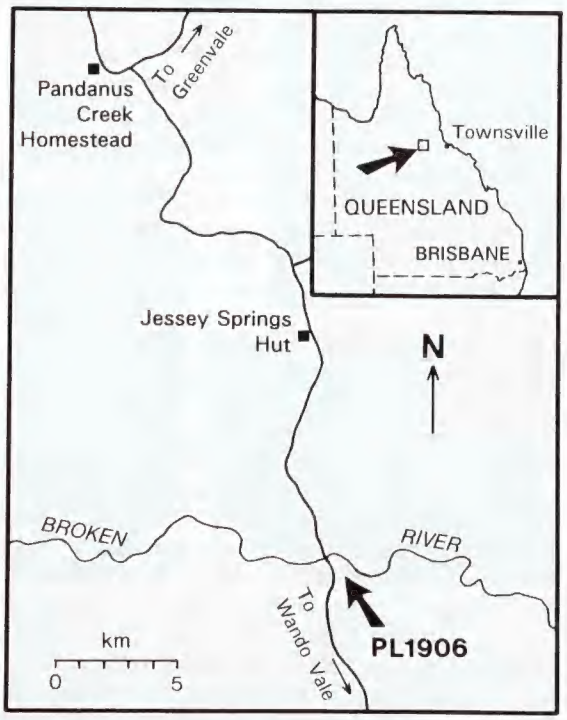



Figure 1. Locality map showing where trilobites were collected from the Poley Cow Formation near Broken River crossing, north Queensland.

internal and external moulds in thinly-bedded, fine micaceous siltstones. The trilobites are disarticulated and commonly broken, indicating that they are not preserved *in situ* but have been transported or reworked. All the faunal elements are represented by specimens of relatively small size, suggesting that sorting may have occurred. This evidence is consistent with the views of Withnall (1989) and Fielding (1993) that the Poley Cow Formation was deposited in a shallow, off-shore marine shelf environment affected by storm or wave activity.

The trilobite assemblage from PL1906 is consistent with the Late Llandovery age indicated by graptolites and conodonts. *Youngia* is not known to range above the Llandovery, and the species of *Kosovopeltis* and *Gaotania* are closely related to *K. yichangensis* Chang and *G. ovata* Chang, respectively, from the Upper Llandovery of China.

The only trilobites previously described from the Broken River Province are the effaced styginid *Rhaxeros pollinctrix*, the cheirurid *Sphaerexochus*, *Encrinurus*?, a possible warburgelline and an indeterminate calymenid (Lane and Thomas, 1978, 1980), from Late Llandovery strata of the Quinton Formation, a lateral equivalent of the Poley Cow Formation in the Gray Creek area, some 25 km north of the Broken River. Effaced styginids have not been found in the Poley Cow Formation, and the material of the other taxa recorded by Lane and Thomas is mostly too fragmentary for useful comparison. Öpik (in White, 1965: 43) identified *Encrinurus*, two species of undetermined scutelluids (= styginids), *Proetus*?, and *Sphaerexochus* or *Onycopyge* from the Quinton Formation in the same area, though the horizon was incorrectly given as the Wairuna Formation, which is of Ordovician age. Arnold and Henderson (1976) reported that the present whereabouts of these specimens are unknown, and a search of the collections in the Australian Geological Survey Organisation failed to locate them (D. L. Strusz, personal communication), so it is not possible to verify Öpik's identifications.

The only other Llandovery trilobite faunas previously described from Australia are those of the "*Illaenus*" band in the Heathcote district of central Victoria (Öpik, 1953), the Richea Siltstone in the Tiger Range of south-western Tasmania (Holloway and Sandford, 1993), and the Rosyth Limestone near Borenore in central western New South Wales (Fletcher, 1950; if the Rosyth Limestone correlates with the Quarry Creek Limestone and with the lower part of the Boree Creek Formation, as suggested by Pickett, 1982, this fauna may be of early Wenlock age; Bischoff, 1986). The first two of these faunas are very different from that of the Poley Cow Formation. The trilobite assemblage of the "*Illaenus*" band is dominated by the effaced styginid *Thomastus* together with dalmanitids and a phacopid, all of which are absent from the Poley Cow Formation. The Richea Siltstone fauna includes *Decoroproetus*, *Latiproetus*?, *Trimerus*, *Acernaspis*, *Dalmanites*, *Anacaenaspis* and *Dicranurus*, as well as *Maurotarion* and *Gravicalymene* which are shared with the Poley Cow Formation. The Rosyth Limestone contains *Ananaspis*, *Trochurus*, *Batocara* and *Youngia*, the last not being recorded by Fletcher (1950) though present in his collections; the last two genera are shared with the Poley Cow Formation, but the species of *Batocara* is not very similar to *B. fritillum* sp. nov.

## Systematic palaeontology

**Styginidae** Vogdes, 1890

***Kosovopeltis*** Šnajdr, 1958

*Type species. Kosovopeltis svobodai* Šnajdr, 1958, from the Ludlow of Bohemia; original designation.

***Kosovopeltis*** sp.

Figure 2A

*Material.* An incomplete cranidium comprising the left part of the glabella and most of the fixigena.

*Remarks.* The low convexity of the cranidium, the preglabellar furrow that is very shallow laterally and appears to weaken further adaxially, and the rounded (exsag.) anterolateral border suggest assignment to *Kosovopeltis*. A distinctive feature is the deep and rather sharp furrow (lateral border furrow?) running subparallel to the cranidial margin on the front of the fixigena, and meeting the axial furrow just behind the widest part of the frontal lobe. This feature is also present in *K. yichangensis* Chang (1974, pl. 80, fig. 2) from the lower Upper Llandovery of south-west China, suggesting that the two species may be closely related. *K. yichangensis* differs from the present species in lacking a shallower furrow (epiborder furrow?) in front of the very deep one on the front of the fixigena, the axial furrow is more abaxially-concave in outline in front of the occipital furrow, the anterior branch of the facial suture diverges more strongly forwards, and the

**Warburgellinae** Owens, 1973

***Warburgella*** Reed, 1931

*Type species. Asaphus Stokesii* Murchison, 1839, from the Wenlock of England; original designation.

***Warburgella*? sp.**

Figure 2G, H, J–L

*Material.* Two cranidia, a librigena and a pygidium.

*Remarks.* These specimens are tentatively assigned to *Warburgella* because of the strongly waisted glabella with deep S1 and shallow S2 and S3, the rather narrow, subparallel-sided L1 with long axis oblique to the sagittal line, the long palpebral lobe, and the comparatively long pygidium with narrow axis (the narrowness is possibly exaggerated by deformation). Features that are not typical of *Warburgella*, however, are the lack of occipital lobes; the absence of a preglabellar field, transverse preglabellar ridge and tropidium; and the weak forward divergence of the anterior branch of the facial suture. Some of these features are characteristic of *Warburgella* (*Anambon*) Landrum and Sherwin, 1976, a subgenus so far recorded only from the Lower Devonian (see also Chatterton and Perry, 1977). A distinctive feature of the librigena is a weak depression on the field, running subparallel to the lateral margin and curving adaxially posteriorly (Fig. 2K); a similar depression is present in some species of *Prantlia* (see *P. grindrodi* Owens, 1973, pl. 15, figs 3–5).

The present cranidia resemble the proetine *Cyphoproetus* but differ in the rather short (sag., exsag.) occipital ring with no lateral lobes and median tubercle not forwardly placed. If the librigena and pygidium are correctly associated with the cranidium, the poorly defined lateral border furrow, weak depression on the librigenal field and the long pygidium with narrow axis also suggest that this species does not belong to *Cyphoproetus*.

The present pygidium is too poorly preserved for comparison with the warburgelline pygidium figured by Lane and Thomas (1978, pl. 2, figs m, p) from the Quinton Formation in the Gray Creek area of the Broken River Province.

**Aulacopleuridae** Angelin, 1854

*Remarks.* Adrain and Chatterton (1993) included their new genus *Goodsiraspis* in the Rorringtoniidae Owens in Owens and Hammann, 1990 but acknowledged that it resembles members of the Aulacopleuridae in "general proportions", the prominent, fully isolated L1, the number of thoracic segments (14 as opposed to 8 or 9 in rorringtoniids), and the short, broad pygidium with only the first pairs of pleural and interpleural furrows well defined. Other similarities with aulacopleurids are the width of L1, which is much narrower than the adjacent median part of the glabella instead of being approximately the same width as in rorringtoniids; the distance of the palpebral lobe from the axial furrow, which is greater than it is in rorringtoniids; the median swelling on the posterior part of the preglabellar field, which is also developed in *Otarion* (see Adrain and Chatterton, 1994, fig. 12.5–12.7), *Songkania* (see Ludvigsen and Tripp, 1990, pl. 8, fig. 3) and more weakly in *Maurotarion* (see Thomas, 1978, pl. 8, fig. 1a, b); and the anterior border furrow that is flexed medially.

Reasons cited by Adrain and Chatterton (1993: 1637) for the assignment of *Goodsiraspis* to the Rorringtoniidae are the deep S2, the rostral plate that does not taper to a point posteriorly, the genal spine that is flattened at its base and carries extensions of the lateral and posterior border furrows, the absence of a "lobate" eye socle, and the apparent absence of posterior spines on the hypostome. None of these points provides grounds for exclusion of the genus from the Aulacopleuridae. S2 appears to be very variable in development in *Goodsiraspis*; in most specimens of the type species, *G. packardi*, it is certainly wider (tr.) and deeper than is normal for aulacopleurids, but in other specimens it is weak (e.g., Adrain and Chatterton, 1993, pl. 1, fig. 1, pl. 2, fig. 9). S2 is also very weak in "*Harpidella*" *butorus* Holloway and "*Cyphaspis*" *novella* Barrande, both of which were assigned to *Goodsiraspis* with question by Adrain and Chatterton, and which I consider to be undoubtedly congeneric with *G. packardi*. The rostral plate does not taper to a point posteriorly in all aulacopleurids; in *Rhinotarion* (see Whittington and Campbell, 1967, pl. 4, fig. 11) and possibly also in *Maurotarion axitiosum* (Campbell, 1977: 16, pl. 3, fig. 2c) the posterior ends of the connective suture are widely separated, as in *Goodsiraspis*. The flattening of the genal spine in *G. packardi* appears to be at least partly due to collapse under post-depositional compression, as shown by the presence of longitudinal fractures and/or depressions along most spines (e.g., Adrain and Chatterton, 1993, pl. 1, figs 1, 4, 5, 7, 8, pl. 2, figs 1, 4). Fracturing also seems to account for the apparent extension of the lateral border furrow

frontal lobe is poorly differentiated from the anterior and lateral borders.

**Proetidae** Salter, 1864

**Proetinae** Salter, 1864

***Proetus*** Steininger, 1831

*Type species. Calymmene concinna* Dalman, 1827, from the Wenlock of Gotland; original designation.

***Proetus*** (s.l.) sp.

Figure 2B–F, I

*Material.* A cranidium, a librigena and 2 pygidia.

*Remarks.* This species is characterised by an elongate, gently forwardly tapering glabella that is well rounded anteriorly; occipital lobes that are weak or absent; no preglabellar field; an apparently weakly forwardly diverging anterior branch of the facial suture; a librigenal field that is narrower than the lateral border; a short genal spine; and a pygidium with a poorly defined border that expands strongly posteromedially. The elongate shape of the glabella has probably been exaggerated by deformation. The weak or absent occipital lobes would exclude the species from *Proetus* (*Proetus*) *sensu* Owens (1973: 11). No similar species has previously been recorded from the Silurian of Australia.

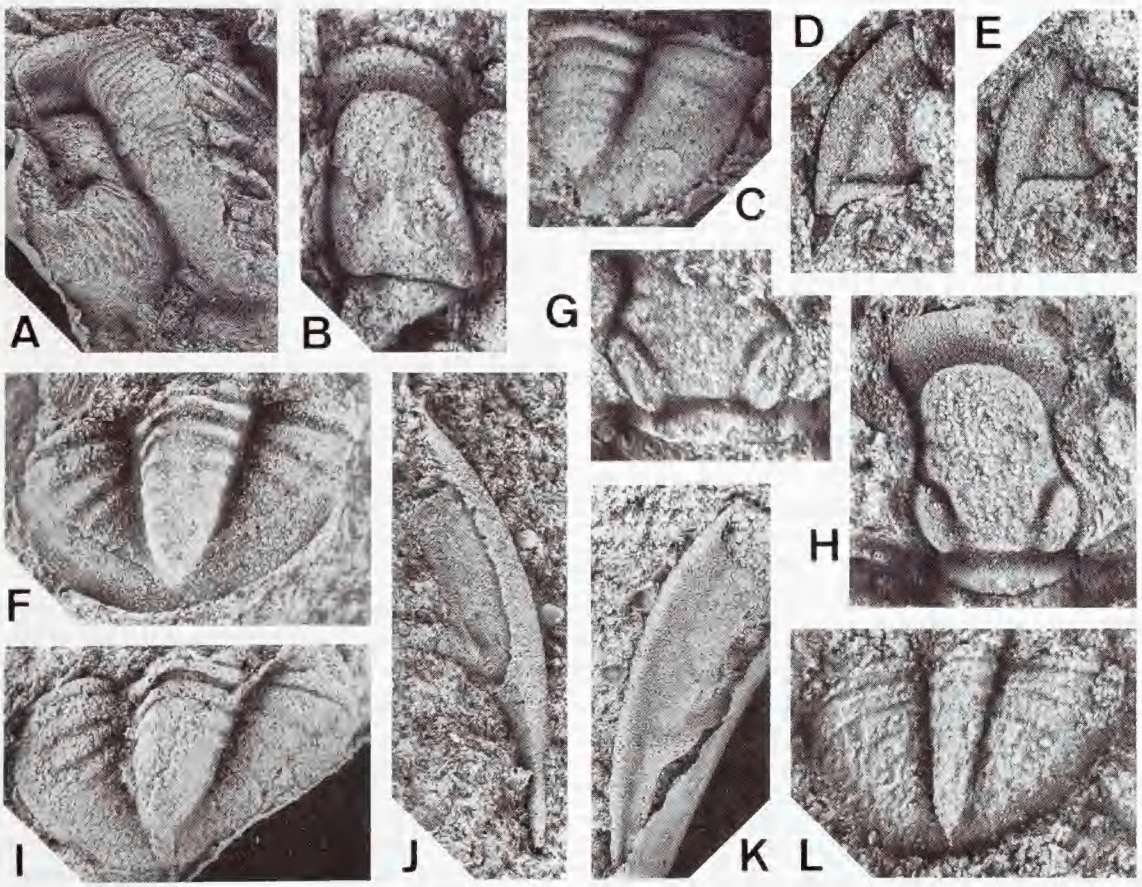



Figure 2. A, *Kosovopeltis* sp., cranidium NMV P134800, latex cast of external mould, dorsal view, × 4. B–F, I, *Proetus* (s.l.) sp. B, cranidium NMV P134801, latex cast of external mould, dorsal view, × 10. C, pygidium NMV P134805, latex cast of external mould, dorsal view, × 10. D, E, librigena NMV P134803, internal mould and latex cast of external mould, dorsal view, × 9. F, I, pygidium NMV P134804, internal mould and latex cast of external mould, × 7. G, H, J–L, *Warburgella* sp. G, cranidium NMV P134809, internal mould, dorsal view, × 8. H, cranidium NMV P134808, internal mould, dorsal view, × 8. J, K, librigena NMV P134810, latex casts of counterpart moulds, ventral and dorsal views, × 6. L, pygidium NMV P134811, internal mould, dorsal view, × 9.

onto the genal spine in Adrain and Chatterton's pl. 1, fig. 7; the true lateral border furrow is seen to meet the posterior border furrow in front of the spine base, and only a single furrow extends along the spine, as is common in aulacopleurids. Adrain and Chatterton (1993, 1994) did not explain their use of the terms "lobate" and "bilobate" for the eye socle of aulacopleurids, but "bilobate" apparently refers to a socle that is considerably wider and/or more convex anteriorly and posteriorly than at midlength (exsag.). The socle of *G. packardi* is poorly defined but does not appear to be bilobate. The socle in *Rhinotarion* is not bilobate either but parallel-sided (Whittington, 1992, pl. 102, figs A, C, D), indicating that a bilobate socle is not a synapomorphy of Aulacopleuridae as indicated by Adrain and Chatterton (1993, fig. 2) in their cladogram. Finally, the only hypostomes of *G. packardi* known are too incomplete to be certain that posterior spines are not present.

*Goodsiraspis* is consequently here assigned to the Aulacopleuridae and is considered to be most closely related to *Maurotarion*. Characters uniting these two genera, and collectively differentiating them from all other aulacopleurids, are the moderate cranidial convexity, the subtrapezoidal or parabolic glabella that is not markedly indented laterally at the front of L1, the relatively short (sag.) preglabellar field, the position of the eye with its midlength (exsag.) opposite the outer end of S1, and the pygidium with the axis as wide anteriorly as the pleurae.

### ***Maurotarion*** Alberti, 1969

*Type species. Harpidella maura* Alberti, 1967, from the lower Ludlow of Morocco; original designation.

*Diagnosis.* See Holloway and Sandford (1993).

### ***Maurotarion*** sp.

Figure 3A, B, E–G, I

*Material.* Four cranidia and 4 librigenae.

*Remarks.* In the subquadrate glabella with more or less transverse anterior outline, the small L1, the anterior border furrow that is uniformly curved in dorsal view instead of having maximum curvature medially, and the anterior border that is not expanded medially, the cranidia resemble those of *Maurotarion christyi* (Hall, 1864) from the Wenlock of Indiana (see Hall, 1879, pl. 32, figs 5–7), *M. hama* (Šnajdr, 1984) from the Wenlock of Bohemia and *M. plautum* (Whittington and Campbell, 1967) from the Upper Wenlock or Ludlow of Maine. Compared with those species, the anterior borders of the present cranidia are more convex (sag., exsag.) and upturned, especially medially, and the anterior border furrow is deeper, but these differences may be due to slight deformation by longitudinal compression. Librigenae assigned to this species differ from those assigned to *Otarion* sp. in having the lateral margin only weakly incurved at the base of the genal spine, and the facial suture crossing the posterior border farther from the genal spine.

*Maurotarion rhaptomyosa* (Sun, 1990) from the Rainbow Hill Marl Member (Ludlow) of the Yass Basin, New South Wales, differs from the present species in having a more elongated and anteriorly-rounded glabella, a larger L1, a less steeply inclined preglabellar field, a shallower anterior border furrow and a flatter anterior border. *M. bowningense* (Mitchell, 1887) from the Lochkovian of the Yass Basin appears to be similar to the present species but the published illustrations are very poor. *M. bowningense* was based on a single specimen (Mitchell, 1887: 438, pl. 16, fig 3; Chatterton, 1971, pl. 24, fig. 10), which is thus the holotype; the designation of a different specimen as lectotype by Chatterton (1971: 96) is invalid.

### ***Otarion*** Zenker, 1833

*Type species. Otarion diffractum* Zenker, 1833, from the Ludlow of Bohemia; by monotypy.

*Remarks.* Adrain and Chatterton (1994) have revised *Otarion* and sought to distinguish it from the closely related *Cyphaspis* Burmeister, 1843. Evaluation of their concepts of both taxa must await publication of their forthcoming work on *Cyphaspis*.

### ***Otarion*** sp.

Figure 3C, D, H, J–L

*Material.* Four cranidia and 4 librigenae.

*Remarks.* Distinctive features are the moderately inflated glabella that narrows weakly forwards in front of L1 and is broadly rounded anteriorly, the very small and laterally projecting L1, the weakly curved S1, the convex and steeply inclined preglabellar field that is approximately equal in length (sag.) to the anterior border plus anterior border furrow, the rather dense cranidial sculpture of fine tubercles, and the librigena with wide (tr.) field

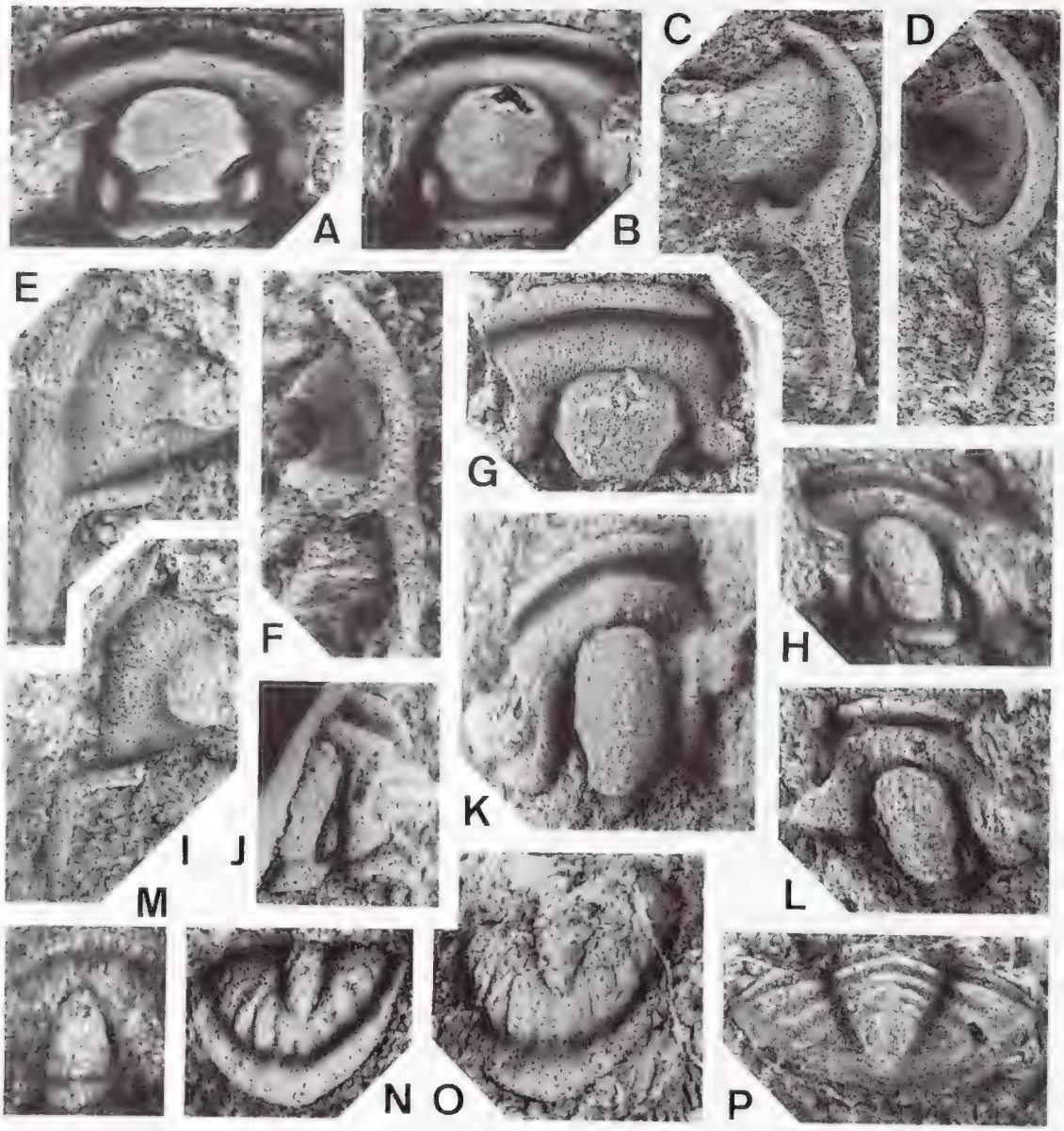



Figure 3. A, B, E–G, I, *Maurotarion* sp. A, cranidium NMV P134816, internal mould, dorsal view, × 6.5. B, G, cranidium NMV P134817, internal mould and latex cast of external mould, dorsal views, × 8. E, librigena NMV P134819, latex cast of external mould, dorsal view, × 10. F, librigena NMV P134835, latex cast of natural mould, ventral view, × 9. I, librigena NMV P134821, latex cast of external mould, dorsal view, × 8. C, D, H, J–L, *Otarion* sp. C, librigena NMV P134814, latex cast of external mould, dorsolateral view, × 8. D, librigena NMV P134815, latex cast of external mould, ventrolateral view, × 8. H, L, cranidium NMV P134812, internal mould and latex cast of counterpart mould, dorsal views, × 10 and × 11.5. J, cranidium NMV P134802, latex cast of external mould, dorsal view, × 9.5. K, cranidium NMV P134813, latex cast of external mould, dorsal view, × 9. M–O, *Scharyia* sp. M, cranidium NMV P134823, internal mould, dorsal view, × 12. N, pygidium NMV P134825, latex cast of external mould, dorsal view, × 12. O, pygidium NMV P134824, latex cast of external mould, dorsal view, × 12. P, Aulacopleuridae indet., pygidium NMV P134822, internal mould, dorsal view, × 9.

and with the lateral margin strongly incurved at the base of the genal spine. In these features there is a similarity to species such as *Otarion brauni* Perry and Chatterton, 1979 and *O. huddyi* Adrain and Chatterton, 1994, both from the Wenlock of Canada, and *O. coppinsensis* Adrain and Chatterton, 1994 from the Wenlock of the Australian Capital Territory. The present material, however, is inadequate for detailed comparison with other species.

*Otarion coppinsensis* was based on specimens considered by Chatterton and Campbell (1980: 87) to be closely related to or possibly conspecific with *Cyphaspis horani* Etheridge and Mitchell (see Chatterton, 1971: 95, pl. 24, figs 1–6; Chatterton and Campbell, 1980, pl. 11, figs 13, 14), from the Ludlow of the Yass district, New South Wales. Adrain and Chatterton (1994: 320) stated of *horani* that it "has 11 thoracic segments, a strongly inflated, but not elongate, glabella, and a pygidium which is narrow relative to its length, bears three axial rings, and has both rings and posterior pleural bands ornamented with single rows of relatively coarse tubercles. All of these make its assignment to *Cyphaspis* unambiguous, and serve to differentiate it from the older Coppins Crossing species" (i.e. *O. coppinsensis*). However, no complete (or even incomplete) thoraces of *coppinsensis* are known, so the number of thoracic segments is indeterminate; there is no appreciable difference from *horani* in the length and inflation of the glabella or in the width of the pygidium; the number of pygidial axial rings is the same as in *horani*; and rows of tubercles are present on the axial rings and posterior pleural bands of both species. Hence none of these features can be used to distinguish *horani* from *coppinsensis*, or to justify assignment of these species to separate genera.

**Aulacopleuridae indet.**

Figure 3P

*Remarks.* The only aulacopleurid pygidium found is transversely lenticular in outline, with an axis that is as wide anteriorly as the pleurae and narrows strongly backwards, six or possibly seven axial rings, four pleural furrows, and a poorly defined border. It is uncertain as to which of the two preceding species this pygidium belongs.

**Scharyiidae** Osmólska, 1957

*Remarks.* Thomas and Owens (1978) included the Scharyiinae in the Aulacopleuridae, but Owens (in Owens and Hammann, 1990) transferred it to the Brachymetopidae. I follow Adrain and Chatterton (1993) in regarding Scharyiidae as a separate family within the Aulacopleuroidea.

***Scharyia*** Přibyl, 1946

*Type species. Proetus micropygus* Hawle and Corda, 1847, from the Ludlow of Bohemia; original designation.

***Scharyia*** sp.

Figure 3M–O

*Material.* A cranidium and 2 pygidia.

*Remarks.* The conical glabella lacking furrows, the long preglabellar field, and the rather long pygidium indicate that these poorly preserved specimens belong to *Scharyia*. The pygidia resemble that of *S. redunzoi* Perry and Chatterton, 1979 from the Wenlock of Canada in having interpleural furrows that are much deeper than the pleural furrows (except for the first pleural furrow; see Fig 3O), a prominent border and a deep border furrow; *S. redunzoi* differs, however, in that the axis extends closer to the border furrow posteriorly, the border does not expand posteromedially, and the posterior margin is not subangular medially.

**Cheiruridae** Hawle and Corda, 1847

**Acanthoparyphinae** Whittington and Evitt, 1954

***Youngia*** Lindström, 1885

*Type species. Cheirurus trispinosus* Young, 1868, from the Llandovery of Scotland; subsequent designation of Vogdes (1917: 115).

*Remarks.* Several species previously included in *Youngia* were reassigned by Ramsköld (1983) and Chatterton and Perry (1984) to *Hyrokybe* Lane, 1972. There has been confusion in the discrimination of these genera because they share similar cephalic morphology and because no pygidia are known for either type species. New diagnoses for *Youngia* and *Hyrokybe* were given by Chatterton and Perry (1984) on the basis of new material of a number of species, most represented by both cephala and pygidia. The pygidia of species they assigned to *Hyrokybe* have two pairs of marginal spines of almost equal size, and are very different from the pygidia assigned to *Youngia* which have the

outer pair of spines greatly elongated and the inner pair very reduced in size. Although Chatterton and Perry did not list differences between the two genera, comparison of their diagnoses and discussion suggests that, in addition to the form of the pygidial spines, they considered *Hyrokybe* to differ from *Youngia* in that the occipital and genal spines are commonly shorter, there are two pairs of secondary spines on the lateral fixigenal border in front of the genal spine, the hypostome is commonly fused to the rostral plate, and the posterior margin of the hypostome has a series of blunt spines medially. Secondary spines on the lateral fixigenal border are apparently not present, however, in the type species of *Hyrokybe, H. pharanx* Lane (1972, pl. 64, figs 1–3). Species assigned by Chatterton and Perry to *Hyrokybe* also differ from those assigned to *Youngia* in that the glabella (excluding the occipital spine) is always wider than long in dorsal view (in *Youngia* the glabella is commonly as wide as long or slightly longer than wide, but in *Y. johnsoni* it is wider than long), and the middle furrow of the hypostome is weaker and directed transversely or slightly obliquely forwards rather than obliquely backwards. The differences in the cranidium are not always consistently developed, so that in the absence of hypostomes or pygidia unequivocal assignment to *Youngia* or *Hyrokybe* may not be possible.

***Youngia*** sp.

Figure 4

*Material.* A cephalon, 6 cranidia, 3 isolated fixigenae, 3 librigenae, and a hypostome.

*Remarks.* S3 is distinguishable on only one of the cranidia (Fig. 4L), in which, however, S2 is obliterated by a fracture. S3 is more anteriorly directed than S1 and S2, and meets the axial furrow at the abaxial end of the preglabellar furrow.

This species, which in the absence of pygidia is not formally named, is assigned to *Youngia* rather than to *Hyrokybe* because the glabella is approximately as wide as long (sag.) in dorsal view, the occipital and genal spines are relatively large, the hypostome has a well-defined middle furrow that is directed obliquely backward, and the posterior margin of the hypostome is not spinose medially. The type species, *Y. trispinosa*, differs from the present one in having longer occipital and genal spines, the occipital spine is thicker at its base, the eye is situated farther forwards with its posterior edge opposite S1, and the lateral border furrow is indistinct near the genal angle (Lane, 1971, pl. 16, figs 1–4, 7–9, 11, 13).

Of the species assigned to *Youngia* by Chatterton and Perry (1984) from the Upper Llandovery of Canada, those most closely resembling the present one are *Y. boucoti, Y. kathyae* and *Y. steineri*. These three species, considered by Chatterton and Perry to belong to a single evolutionary lineage, differ from the Poley Cow species in that S1 does not meet the occipital furrow, the fixigenae are narrower so that the genal spine arises closer to the occipital ring, and the palpebral lobe is situated farther forwards with its posterior edge opposite S1. The hypostome of *Y. boucoti* is unknown, but those of *Y. kathyae* and *Y. steineri* differ from the hypostome of the Poley Cow species in having more pronounced tubercles on the anterior lobe of the middle body.

**Sphaerexochinae** Öpik, 1937

***Sphaerexochus*** Beyrich, 1845

*Type species. Spaerexochus* [sic] *mirus* Beyrich, 1845, from the Wenlock of Bohemia; by monotypy.

***Sphaerexochus*** sp.

Figure 5A–G, I, J

*Material.* Eight cranidia, a hypostome, an incomplete thoracic segment and a pygidium.

*Remarks.* Numerous *Sphaerexochus* species have been named from the Silurian but their discrimination is made difficult by conservatism in cephalic morphology (Holloway, 1980: 38) and variability in the pygidium. Pygidial variation has in some cases been attributed to dimorphism (Perry and Chatterton, 1977; Ramsköld, 1983; Chatterton and Perry, 1984) and in other cases to the type of preservation or to changes during ontogeny (Thomas, 1981). These factors, together with the poor preservation of the present material and the paucity of pygidia, make reliable comparison with other species impossible.

Nevertheless, several species resemble the present one in having a relatively broad pygidium with very short marginal projections and distinct pits in the axial furrow near the front of the terminal lobe. Such species include *S. britannicus* Dean, 1971 from the Wenlock of England (if this is distinct from *S. mirus*; see Thomas,

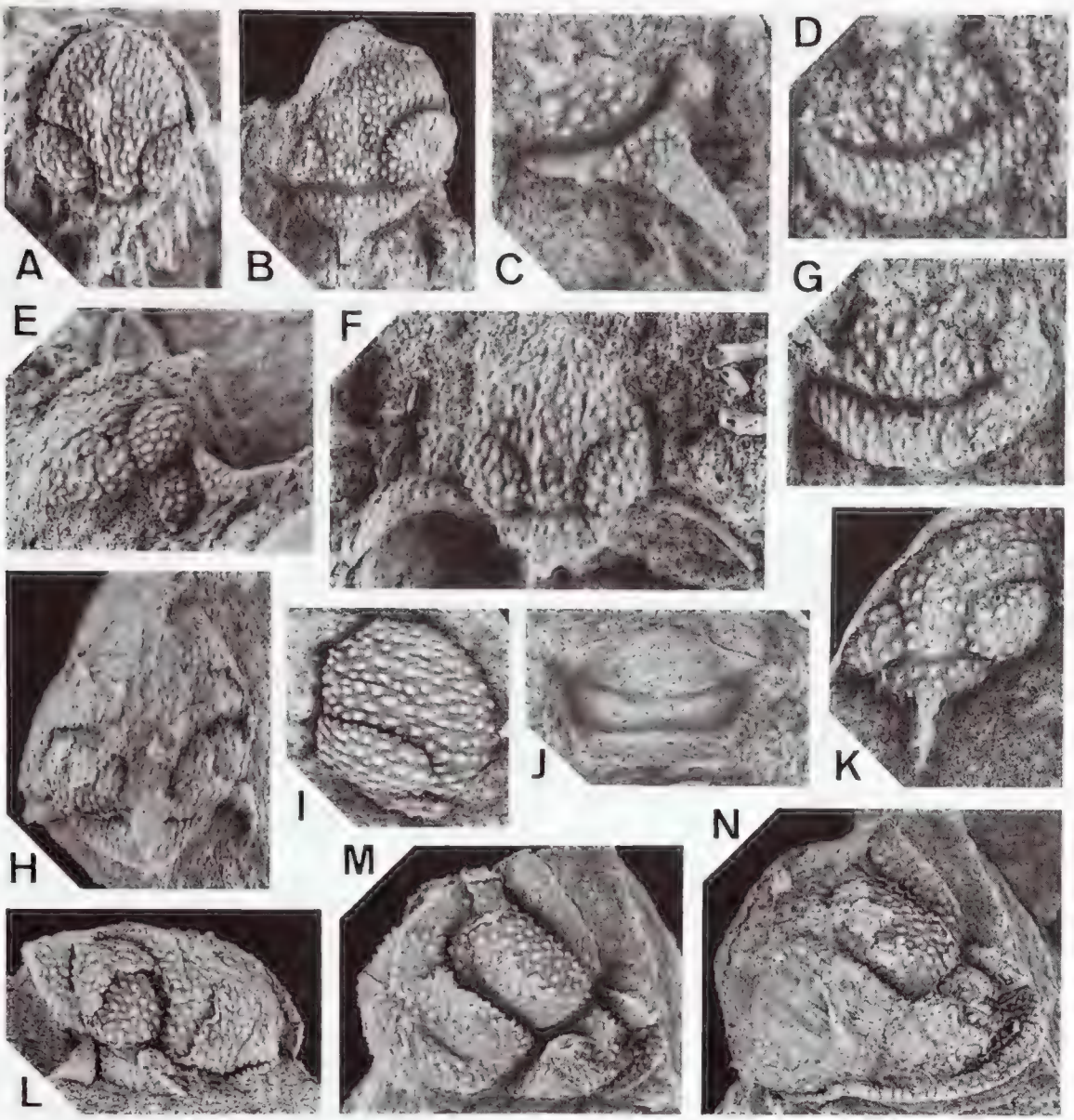



Figure 4. *Youngia* sp. A, cranidium NMV P134828, latex cast of external mould, external view, × 5. B, cranidium NMV P134830, internal mould, dorsal view, × 4. C, fixigena NMV P134834, latex cast of external mould, oblique view (posterior border at bottom of photograph), × 6. D, librigena NMV P134839, latex cast of external mould, oblique view, × 10. E, F, cranidium NMV P134827, latex cast of external mould, oblique and external views, × 6. G, librigena NMV P134838, latex cast of external mould, oblique view, × 6. H, L–N, incomplete cephalon NMV P134826; H, L, N, latex cast of external mould, dorsal, lateral and oblique views (anterior lateral glabellar furrow in L is S3), × 3; M, internal mould, oblique view, × 3. I, cranidium NMV P134832, latex cast of external mould, oblique view, × 4. J, hypostome NMV P134840, latex cast of external mould, ventral view, × 2. K, cranidium NMV P134829, latex cast of external mould, dorsal view, × 4.

1981), *S. glaber* Holloway, 1980 from the Wenlock of Arkansas and Oklahoma, *S. scabridus* Angelin, 1854 from the Wenlock of Gotland (see Ramsköld, 1983), and Ramsköld's (1983, pl. 28, figs 1a, b, 6a, b) pygidial dimorph B of *S. latifrons* Angelin, 1854, from the Ludlow of Gotland. The last of these is perhaps the most similar but, compared with the present species, the glabella of *S. latifrons* seems to be much wider adaxial to L1 (Ramsköld, 1983, pl. 27, fig. 12b). Pygidia of *S. britannicus* and *S. scabridus* have a more convex (sag.) axial terminal lobe that is semielliptical or bulbous rather than subtriangular, and the third marginal projection is longer. In addition, the hypostome of *S. scabridus* has a more convex anterior margin, a lateral border not expanding as strongly backwards, and a deeper, more concave-forwards posterior border furrow (Ramsköld, 1983, pl. 27, figs 7, 8). The pygidium of *S. glaber* has a more convex (sag.) terminal lobe, and the third pleural rib does not project distally at all.

Chatterton and Campbell (1980) described two Australian species, *Sphaerexochus molongloensis* from the Wenlock of Canberra and *S. lorum* from the Ludlow of the Yass Basin, New South Wales. The former is the more similar to the present species but appears to have a longer pygidium with a more distinct pseudo-articulating half ring on the second segment, and a longer third marginal projection.

**Deiphoninae** Raymond, 1913

***Sphaerocoryphe*** Angelin, 1854

*Type species. Sphaerocoryphe dentata* Angelin, 1854, from the Upper Ordovician of Sweden; ICZN Opinion 614 (*Bulletin of Zoological Nomenclature* 18: 357).

***Sphaerocoryphe*** sp.

Figure 5H, K

*Material.* Internal moulds of a cranidium and a pygidium, on the same piece of rock.

*Remarks.* Distinctive features are the glabellar bulb that is wider than long; the very short (sag.) L1; the widely divergent genal spine (very poorly preserved as an external mould of the ventral surface); the stout, downwardly directed profixigenal spine (preserved as a pit in Fig. 5H; the slightly smaller pit to the right of it is not another spine); the shallow subgenal notch; the relatively long and weakly curved first pygidial marginal spine; the second marginal spine that is flexed backwards distally; the narrow, transverse posterior pygidial margin between the second pair of spines; and the deep pygidial axial furrow behind the second ring. In the pygidial characters listed above there are similarities with *Deiphon*, a genus generally considered to have been derived from *Sphaerocoryphe* (Lane, 1971; Holloway and Campbell, 1974; Chatterton and Perry, 1984; Přibyl et al., 1985). The present species is assigned to *Sphaerocoryphe* rather than to *Deiphon* because the fixigena is not markedly reduced in size, there is a well developed posterior cephalic border, and the subgenal notch is only very shallow. Further assessment of relationships must await the availability of better material.

A short, third pair of pygidial spines is present in most, if not all, deiphonines (Holloway, 1980) but has not been seen on the present pygidium. In *Deiphon* and at least some species of *Sphaerocoryphe* these spines are ventrally directed and consequently are not visible unless the entire posterior margin of the pygidium is excavated. Such excavation was considered inadvisable in the case of the present pygidium because of likely damage to the internal mould of the dorsal surface.

The only previous record of *Sphaerocoryphe* from strata younger than Ashgill was by Thomas and Lane (1983: 62), who mentioned its occurrence at an unspecified horizon in the Silurian.

**Encrinuridae** Angelin, 1854

**Encrinurinae** Angelin, 1854

***Prostrix*** gen. nov.

*Etymology.* Latin *pro*, forward, and *strix*, furrow, referring to the deep longitudinal median furrow on the frontal lobe of the type species. Gender feminine.

*Type species. Prostrix amnicola* sp. nov., from the upper Llandovery of north Queensland.

*Diagnosis.* Glabella of low convexity; L1 continuous across glabella; S1–S3 and preglabellar furrow deep and slit-like abaxially but weak medially; frontal lobe with deep longitudinal median furrow anteriorly. Glabellar tubercles weak on external surface but distinct internally, longitudinally paired on L2–L4; anterior cranidial border with a few small, weak tubercles. Palpebral lobe long (exsag.), situated close to glabella with posterior edge opposite median part of occipital furrow and anterior edge opposite

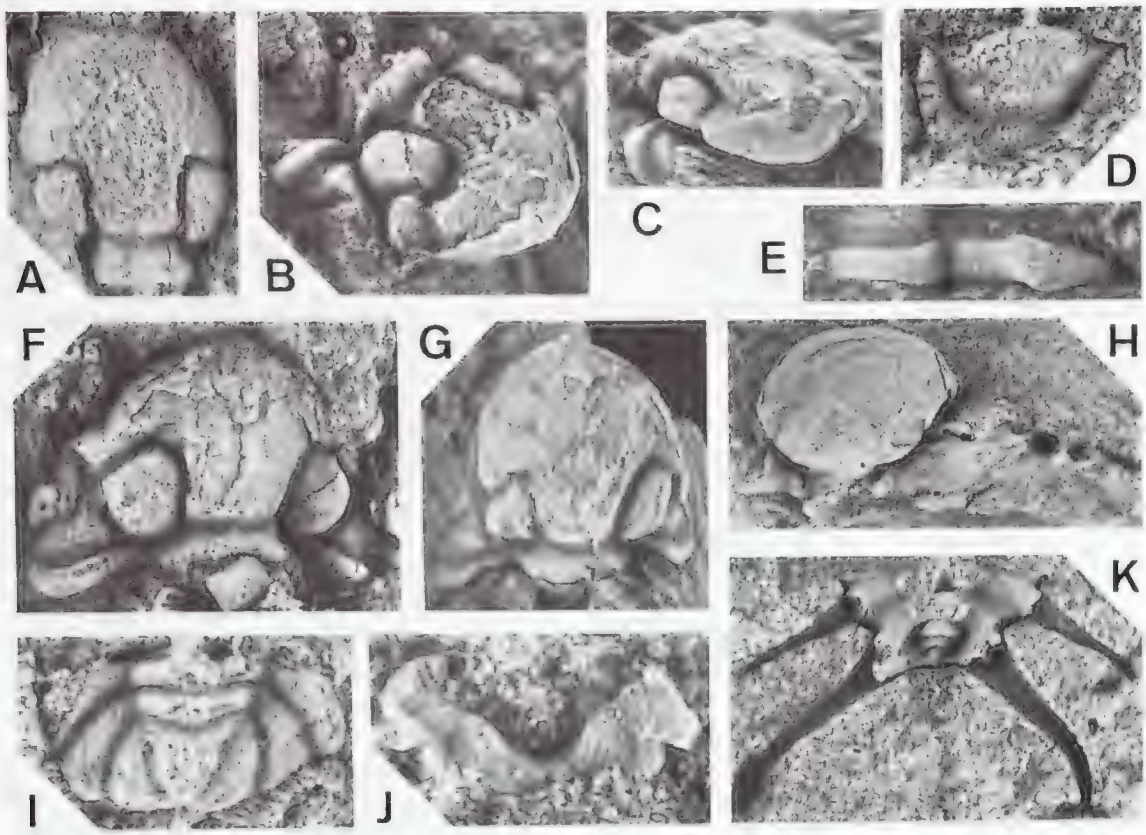



Figure 5. A–G, I, J, *Sphaerexochus* sp. A, cranidium NMV P134842, latex cast of external mould, dorsal view, × 5. B, F, cranidium NMV P134841, internal mould and latex cast of external mould, oblique and dorsal views, × 5.5. C, G, cranidium NMV P134843, internal mould, oblique and dorsal views, × 5. D, hypostome NMV P134849, latex cast of external mould, ventral view (ridge extending forward from median part of anterior margin is preparation mark), × 6. E, thoracic segment NMV P134850, internal mould, oblique view, × 6. I, J, pygidium NMV P134851, latex casts of counterpart moulds, dorsal and ventral views, × 9. H, K, *Sphaerocoryphe* sp. H, cranidium NMV P134853, internal mould, dorsal view, × 4. K, pygidium NMV P134854, broken internal mould, dorsal view, × 5.

S3, with small circular pit at midlength; palpebral furrow almost exsagittally aligned except anteriorly and posteriorly. Fixigenal field without distinct tubercles; genal spine absent. Hypostome with poorly defined rhynchos. Pygidium with 12+ axial rings and 9 or possibly 10 pleural ribs not projecting strongly distally. Doublure sloping steeply downwards and inwards towards front of pygidium.

*Remarks.* The genus is known only from the rather poorly preserved type species, whose relationship with other encrinurines is uncertain. With the discovery of additional species, some characters included in the preceding diagnosis may prove to be significant only at species level. Other characters included are primitive for Encrinurinae (e.g., presence of preglabellar furrow and longitudinal median furrow, abaxially slit-like lateral glabellar furrows, L1 continuous across glabella rather than obsolete medially, glabellar tubercles longitudinally paired on L2–L4), so that their presence in other taxa (e.g., *Cromus* Barrande, 1852, *Perryus* Gass and Mikulic, 1982; see Edgecombe and Chatterton, 1992) is not necessarily indicative of close relationship.

*Prostrix* differs from *Batocara* Strusz, 1980, to which most other Australian Silurian encrinurines are assigned herein (see below), in that the glabella is less convex, the glabellar and preglabellar furrows are wider (tr.) and slit-like abaxially, the longitudinal median furrow is well defined, L2–L4 are not tuberculiform but have

longitudinally paired tubercles, the tuberculation is weak on the exterior of the glabella (Fig. 6A, K) and on the anterior cranidial border, the palpebral lobe is situated very close to the glabella and to the posterior border furrow, the fixigenal field lacks distinct tubercles, the hypostome has a poorly defined rhynchos, and there are fewer axial rings in relation to the number of pleural ribs.

*Prostrix* resembles some of the Chinese Llandovery encrinurine species that have been assigned to *Encrinuroides* Reed, 1931, but whose affinity with that genus was considered dubious by Edgecombe and Chatterton (1990a). The greatest similarity is with species such as "*Encrinuroides*" *abnormis* Chang, 1974, "*E.*" *enshiensis* Chang, 1974 (both revised by Chang, 1986), "*E.*" *guangyuanensis* Chang, 1986 and "*E.*" *renhuaiensis* Yin in Yin and Lee, 1978. Similarities include the abaxially slit-like glabellar and preglabellar furrows, the moderate-sized glabellar tubercles that in some species are longitudinally paired on L2–L4, and the absence of genal spines (in species with the genal angles preserved). The Chinese species differ from *Prostrix*, however, in having stronger tuberculation on the glabella and anterior cranidial border, the eye is situated farther from the glabella and from the posterior border furrow, there are prominent tubercles on the fixigenal field, and the pygidium has a greater number of axial rings in relation to the number of pleurae.

*Langgonia* Kobayashi and Hamada, 1971, known from three species (probably synonymous) from the upper Llandovery or lower Wenlock of West Malaysia, was originally placed in the Dalmanitidae but was transferred to the Encrinuridae by Holloway (1981). *Langgonia* resembles *Prostrix* in the abaxially slit-like glabellar and preglabellar furrows, the distinct longitudinal median furrow on the front of the glabella, L1 that is continuous across the glabella, the weak tuberculation on the glabellar exterior, the closeness of the eyes to the glabella, and the absence of genal spines. *Langgonia* differs from *Prostrix* in that the glabella is more convex across the frontal lobe, the palpebral lobe is situated farther forward and more obliquely on the cheek, there are nodular lobes on the posterior part of the fixigena adjacent to the axial furrow, and the pygidium is semi-elliptical rather than subtriangular in outline, with broader pleural lobes and fewer axial rings in relation to the number of pleural ribs.

***Prostrix amnicola*** sp. nov.

Figure 6

*Etymology.* Latin *amnicola*, inhabitant of or by a river, referring to the proximity of the type locality to the Broken River; noun in apposition.

*Type material.* Holotype: cranidium NMV P134833A, B (counterparts), Fig. 6F, K.

Paratypes: NMV P134855, P134857, P134862 (cranidia); NMV P134859–P134861 (hypostomes); NMV P134863–P134865 (pygidia).

*Diagnosis.* As for genus.

*Description.* Glabella flat-topped in transverse profile and weakly convex in lateral profile, expanding gently forwards in front of occipital ring, approximately 1.5 times as wide at frontal lobe as at L1. Occipital ring decreasing slightly in length (exsag.) abaxially, with a slight node distally; occipital furrow deep and gently arched forwards. Preglabellar furrow not as deep as glabellar furrows abaxially, not defined medially on external surface. L1–L3 successively longer exsagittally; frontal lobe comprising half preoccipital length of glabella, lateral extremity partly isolated in holotype by short, weak depression directed forwards from S3 (Fig. 6F). Glabellar tubercles arranged in transverse row on medial part of L2 and posterior part of frontal lobe; arrangement on L3 apparently more variable (Fig. 6E, F). Palpebral lobe occupying most of fixigena, steeply upturned; palpebral furrow narrow and deep. Posterior cranidial margin deflected backwards at fulcrum and recurved forwards distally; posterior border furrow longer (exsag.) and deeper than occipital furrow adaxially, shallowing distally.

Hypostome with elliptical, moderately convex middle body; rhynchos poorly defined, projecting over anterior border furrow but not bounded laterally by furrow; macula distinct.

Pygidium approximately as wide as long (sag.), subtriangular, rounded posteriorly. Axis well-rounded (tr.), approximately as wide as pleural lobe anteriorly; ring furrows deep laterally, shallower medially; sagittal tubercle present on sixth and possibly third rings. Pleurae curving downwards abaxially from axial furrow; pleural ribs flat-topped, first one projecting slightly distally, remainder not projecting; interrib furrows much shorter (exsag.) than ribs. Doublure divided into a flattened, steeply inclined outer portion and an upwardly flexed

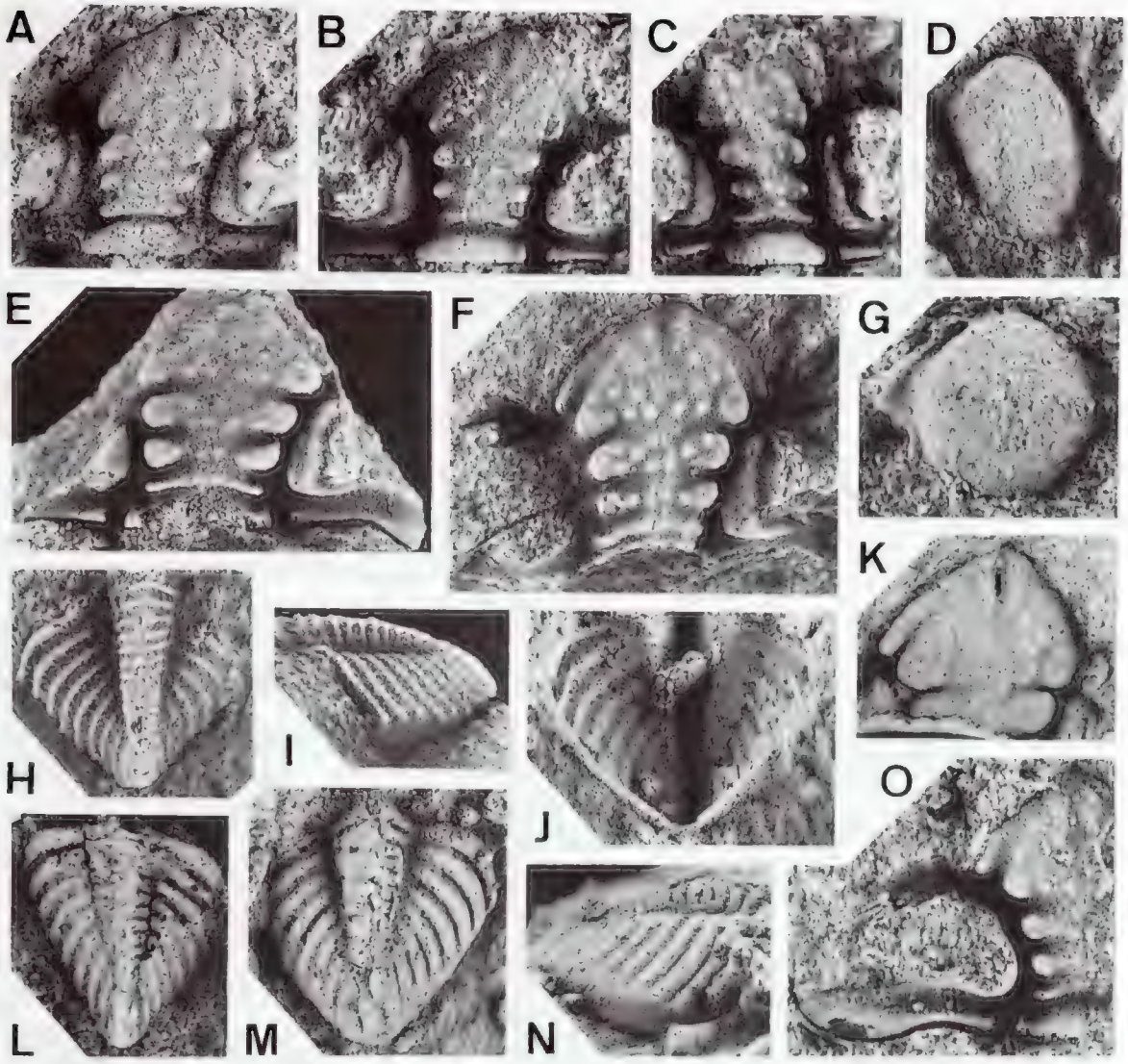



Figure 6. *Prostrix amnicola* gen. nov., sp. nov. A, B, cranidium NMV P134856, latex cast of external mould and internal mould, dorsal views, × 7. C, cranidium NMV P134862, internal mould, dorsal view, × 9. D, hypostome NMV P134860, latex cast of external mould, ventral view, × 7. E, cranidium NMV P134855, internal mould, dorsal view, × 4.5. F, K, cranidium NMV P134833, internal mould and latex cast of external mould, dorsal views, × 4.5. G, hypostome NMV P134861, latex cast of external mould, ventral view, × 8. H, I, pygidium NMV P134864, internal mould, dorsal and lateral views, × 7. J, M, N, pygidium NMV P134863, latex casts of counterpart moulds, ventral, dorsal and lateral views, × 4. L, pygidium NMV P134865, latex cast of external mould, dorsal view, × 6. O, cranidium NMV P134857, internal mould, dorsolateral view, × 6.

inner portion; outer portion very high anteriorly (Fig. 6I, N) but diminishing rapidly posteriorly; inner portion with shallow embayment posteriorly (Fig. 6J).

**_Batocara_** Strusz, 1980

(= *Pacificurus* Ramsköld, 1986a, *pro Australurus* Ramsköld, 1986b, *non* Jell and Duncan, 1986)

*Type species. Encrinurus Bowningi* Foerste, 1888, from the upper Ludlow of New South Wales; original designation.

*Diagnosis.* See Ramsköld (1986b: 559; diagnosis of *Encrinurus* (*Australurus*)).

*Remarks.* Strusz (1980) assigned most Australian and some Asian Silurian encrinurine

species to his *Encrinurus mitchelli* plexus but excluded "*Encrinurus*" *bowningi*, for which he erected *Batocara* as a monotypic genus. Ramsköld (1986a, 1986b) subsequently proposed *Pacificurus* for the *mitchelli* plexus *sensu* Strusz. *Batocara* shares diagnostic characters of *Pacificurus* (L1 continuous across glabella, bearing tubercles adaxially and usually abaxially; L2–L4 tuberculiform and alternating with adaxial tubercles on fixigena; abundant tubercles on genal field and precranidial lobe of librigena; eyes not stalked; genal angle without spines; pygidium relatively large, non-mucronate, with broad pleural lobe), suggesting that *bowningi* shares a common ancestor with species of the *mitchelli* plexus rather than originating in a separate lineage as proposed by Strusz (1980, text-fig. 9). Strusz (1980) considered *Batocara* to be distinguished partly by the coarseness and crowding of the cranidial tuberculation, but amongst species included in *Pacificurus* this character is shared with "*Encrinurus*" *silverdalensis* Etheridge and Mitchell, which also resembles *bowningi* in the prominent median tubercles and well developed sagittal band on the pygidial axis (Strusz, 1980, pl. 5, figs 8–16, pl. 6, figs 5–14). As *bowningi* is evidently closely related to *silverdalensis* and the other Australian species, I consider its separation from them in a monotypic genus to be unjustified. Hence *bowningi* is here included in the *mitchelli* plexus, and *Pacificurus* is regarded as a junior subjective synonym of *Batocara*. The synonymy of *Batocara* and *Pacificurus* was also suspected by Edgecombe and Chatterton (1990b: 4), who listed similarities (some interpreted as synapomorphies) between the two genera, and concluded that *Batocara* is "sister group to *Pacificurus* (if not part of the ingroup)".

***Batocara fritillum*** sp. nov.

Figure 7

*Etymology.* Latin *fritillus*, spotted, referring to the tuberculate cephalon.

*Type material.* Holotype: cranidium NMV P134868A, B (counterparts), Fig. 7B, E.

Paratypes: NMV P134869 (cephalon); NMV P134870, P134871 (cranidia); NMV P134872 (isolated fixigena); NMV P134884, P134885 (librigenae); NMV P134852, P134873–P134882 (pygidia).

*Diagnosis.* Glabella markedly constricted at L2, expanding very strongly forwards in front of L2; front of glabella and anterior cranidial border very steep. Tubercles on posterior part of glabella include I–1,(2); II–1,2; III–1,2,3; iv–1; distal tubercles on L2–L4 not significantly enlarged. Axial furrow wide. Fixigenal field strongly inflated adaxially, with tubercles adjacent to axial furrow not enlarged; 2–3 tubercles situated between posterior edge of palpebral lobe and axial furrow. Librigenal field apparently with only a few tubercles. Pygidium with up to 21 axial rings and 7–10 (usually 9) pleural ribs plus postaxial ridge.

*Description.* Glabella slightly narrower at L2 than at L1 and narrower at L3 than at occipital ring; widths at occipital ring, L2 and L4 approximately in ratio 1.7:1:2. Occipital ring well rounded (sag., exsag.), decreasing in length (exsag.) distally abaxial to L1; occipital furrow deep. S1–S3 continuous across glabella, S3 very shallow medially; distal tubercle on L1 (if present) small and low. Frontal lobe strongly inflated, comprising half sagittal length of glabella in dorsal view, bearing fairly dense tubercles that are of two sizes (Fig. 7B) and not arranged in distinct rows. Preglabellar furrow indistinct or undefined medially; anterior cranidial border complete only on holotype (Fig. 7E), lateral third with 5 tubercles that decrease in size adaxially, median third lacking distinct tubercles. Palpebral lobe upturned, anterior edge opposite L4 and posterior edge opposite L2; palpebral furrow shallow and broad. Eye ridge distinct on internal moulds (Fig. 7E), crossing axial furrow obliquely opposite L4 and with prominent tubercle at abaxial edge of axial furrow. Anterior branch of facial suture not converging as strongly forward as eye ridge; posterior branch transverse adaxially, thereafter flexed posterolaterally in concave-forward curve subparallel to part of posterior cranidial margin. Posteromedial part of fixigenal field standing higher than glabella opposite, with dense tubercles and intervening pits; largest tubercles adjacent to palpebral furrow; fixigenal tubercles very subdued on exterior of large specimens (Fig. 7A). Genal angle rounded.

Librigenal field wider (tr.) than height of lateral border, bearing only a few large tubercles. Base of eye socle higher than precranidial lobe, defined by rather deep furrow. Lateral border behind precranidial lobe with a single row of subdued tubercles; anterior furrow poorly defined; precranidial lobe shorter (exsag.) than librigenal field.

Pygidium slightly longer than wide, posterolateral margins weakly concave in outline. Axis 0.25–0.3 times maximum pygidial width anter-

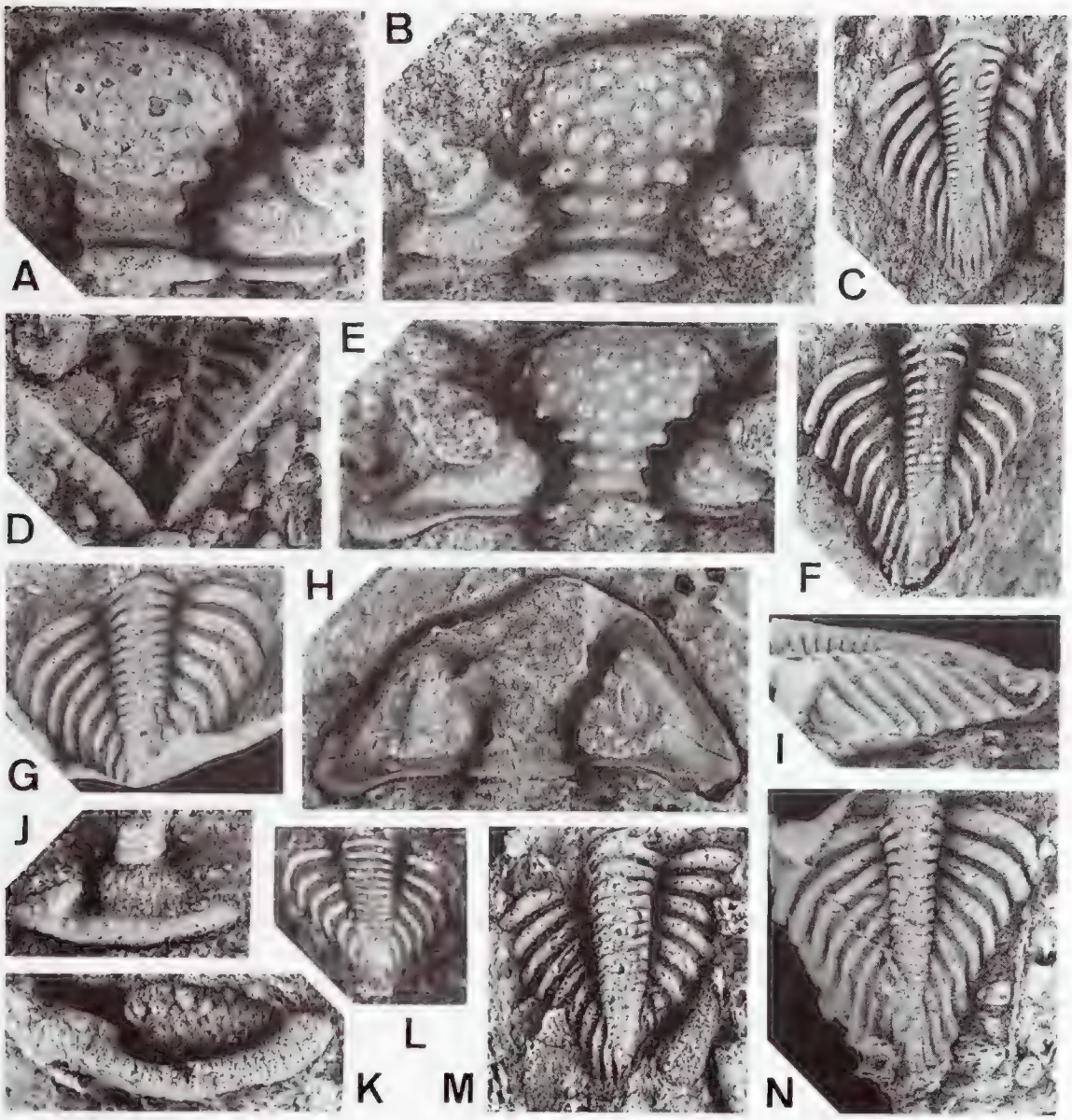



Figure 7. *Batocara fritillum* sp. nov. A, cranidium NMV P134870, latex cast of external mould, dorsal view, × 4.5. B, E, holotype, cranidium NMV P134868, latex cast of external mould and internal mould, dorsal views, × 6.5 and × 5.5. C, pygidium NMV P134873, latex cast of external mould, dorsal view, × 4. D, pygidium NMV P134874, latex cast of natural mould, ventral view, × 6. F, pygidium NMV P134875, internal mould, dorsal view, × 6. G, pygidium NMV P134852, latex cast of external mould, dorsal view, × 5. H, cephalon NMV P134869, internal mould, dorsal view, × 4. I, N, pygidium NMV P134876, latex cast of external mould, lateral and dorsal views, × 4. J, librigena NMV P134884, internal mould, exterior view, × 10. K, librigena NMV P134885, latex cast of external mould, exterior view, × 7. L, pygidium NMV P134877, internal mould, dorsal view, × 7. M, pygidium NMV P134878, latex cast of external mould, dorsal view, × 8.

iorly, tapering backwards rather strongly over first 2–3 segments, thereafter more gently; sagittal band distinct but crossed by shallow medial parts of ring furrows, especially anteriorly. Up to 3 median axial tubercles distinguishable on some pygidia but subdued on exterior; first tubercle on ring 3 or 4, second on third next ring, last on third or fourth next ring. Pleural ribs on anterior segments curving strongly backwards abaxially, on posterior segments becoming more exsagittally aligned and acquiring sigmoidal shape as distal ends turn outwards slightly; ends of ribs form blunt projections (Fig. 7D). Some internal moulds with sparse tubercles along ribs (Fig. 7F). Inter-rib furrows narrower than ribs on external surface. Pygidial doublure widening slightly posteriorly towards V-shaped notch (Fig. 7D).

*Remarks.* The librigena on a poorly preserved cephalon of *Batocara fritillum* has the tubercles on the field arranged in a single row close to the base of the eye (Fig. 7H), whereas two isolated librigenae lack this arrangement of tubercles on the field (Fig. 7J, K). Despite this difference, the isolated librigenae are assigned to *B. fritillum* rather than to *Prostrix amnicola* because the eye appears too small to match the palpebral lobe on the latter species.

*Batocara fritillum* is easily distinguished from most other species of the genus by the marked constriction of the glabella at L2, the inflated frontal lobe that is very steep anteriorly, the wide axial furrow not overhung by enlarged adaxial tubercles on the fixigena, and the sparse tuberculation on the librigenal field. *B. fritillum* resembles *B. bowningi* (see Strusz, 1980, pl. 6, figs 5–14) in the constriction of the glabella at L2, but there are so many other differences between the two species that they are not considered to be closely related.

"*Pacificurus*" *chilorhodus* Edgecombe and Ramsköld, 1992 from the Telychian (not Sheinwoodian; G. D. Edgecombe, personal communication) of Canada resembles *Batocara fritillum* in several respects, notably the constriction of the glabella across L2, the distal tubercles on L2–L4 that are not significantly enlarged, and the non-enlarged adaxial fixigenal tubercles. "*P.*" *chilorhodus* differs from *B. fritillum*, and from all other members of *Batocara*, in having S1 merging with the occipital furrow medially, a pygidium with a low ratio of axial rings to pleural ribs, and distinct paired tubercles on the pygidial axial rings. These characters are shared with *Balizoma* (*sensu* Holloway, 1980 and Ramsköld, 1986b), suggesting that *chilorhodus* may be more closely related to that genus (though not belonging to it) than to *Batocara*.

### **Coronocephalus** Grabau, 1924

*Type species. Encrinurus (Coronocephalus) rex* Grabau, 1924, from the Upper Llandovery (Temple and Wu, 1990) of China; by monotypy.

### ***Coronocephalus*? aff. *urbis*** Strusz, 1980

Figure 8A–F, H–J, L–N

*Material.* Five cranidia, an isolated fixigena, 2 librigenae and 5 pygidia.

*Remarks. Coronocephalus urbis*, from the Wenlock of the Canberra district, was excluded from *Coronocephalus* by Chang (1983: 203, 223) because it has a distinct preglabellar furrow, a shallow longitudinal median furrow on the front of the glabella, and numerous small tubercles on the librigenal margin. However, these characters are primitive homologues of derived states present in most *Coronocephalus* species (preglabellar and longitudinal median furrows weak or effaced, single row of large denticles on librigenal margin) and do not preclude a close relationship with that genus. Consequently *urbis* is here assigned to *Coronocephalus* with question.

The present specimens resemble *Coronocephalus*? *urbis* in the long genal spine, the wide (tr.) anterior cranidial border with a double row of tubercles, the shallow longitudinal median furrow (Fig. 8L), the broad palpebral area, the densely tuberculate librigena with a narrow field, and the relatively short pygidium with distinct sagittal tubercles. The specimens differ from topotypes of *urbis* in having fewer pygidial axial rings (about 14 instead of about 20) and pleural ribs (9–10 instead of 10–11), a distinct anterior furrow on the librigena (Fig. 8C), and possibly in the glabellar tubercle pattern (e.g., the presence of tubercles ii–0 and iii–0 or iii–1 in some cranidia). The Poley Cow species thus appears distinct from *urbis* but the material (especially of cranidia) is considered inadequate for formal naming.

*Coronocephalus*? *thailandicus* (Kobayashi and Sakagami, 1989), from the upper Wenlock or lower Ludlow of Thailand, was considered by Edgecombe and Ramsköld (1992: 261) to be closely related to *urbis*, and shares many of the similarities between that species and the present

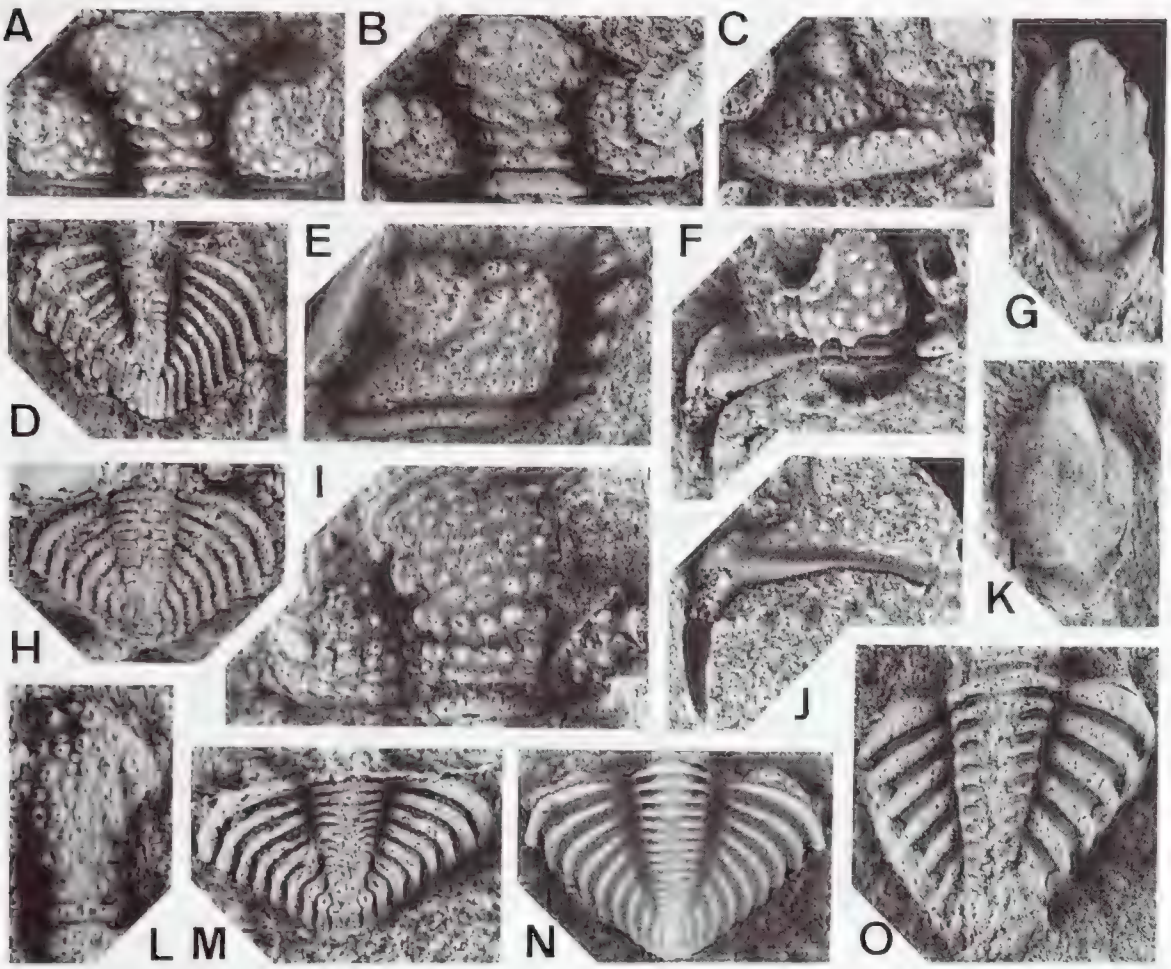



Figure 8. A–F, H–J, L–N, *Coronocephalus*? aff. *urbis* Strusz. A, B, cranidium NMV P134886, internal mould and latex cast of external mould, dorsal views, × 7. C, librigena NMV P134892, latex cast of external mould, exterior view, × 7. D, pygidium NMV P134893, internal mould, dorsal view, × 8. E, cranidium NMV P134887, latex cast of external mould, dorsal view, × 6. F, cranidium NMV P134888, internal mould, dorsal view, × 5. H, pygidium NMV P134894, latex cast of external mould, dorsal view, × 8. I, cranidium NMV P134889, latex cast of partly testiferous mould, dorsal view, × 5. J, fixigena NMV P134890, internal mould, dorsal view, × 5. L, small cranidium NMV P134891, latex cast of external mould, dorsal view, × 10. M, pygidium NMV P134895, latex cast of external mould, dorsal view, × 6.5. N, pygidium NMV P134896, internal mould, dorsal view, × 6. G, K, encrinurid hypostomes indet. G, NMV P134897, internal mould, ventral view, × 7. K, NMV P134898, latex cast of external mould, ventral view, × 6. O, encrinurid pygidium indet., NMV P134899, latex cast of external mould, dorsal view, × 4.

one. *C? thailandicus* is most readily distinguished from the present species by its longer pygidium with a greater number of axial rings.

**encrinurid hypostomes indet.**

Figure 8G, K

*Remarks.* These two hypostomes differ markedly from each other and clearly belong to separate taxa. Both hypostomes have a rhynchos that projects strongly anteriorly and is bounded laterally by deep furrows, but in one specimen the rhynchos is conical (Fig. 8K) whereas in the other it narrows weakly forwards, is broadly rounded anteriorly and slightly concave in outline laterally (Fig. 8G). The specimens also differ in the length (sag.) of the posterior border and the curvature of the posterior margin.

It is not possible confidently to match these hypostomes with the two preceding species. *Cor-*

*onocephalus*? *urbis* has a conical rhynchos, as do most species of *Batocara*. However, *Batocara silverdalense* (Etheridge and Mitchell) has a rather weakly tapering rhynchos (Strusz, 1980, pl. 5, fig. 14), suggesting that the present hypostome with this character may belong to *B. fritillum*.

**encrinurid pygidium indet.**

Figure 8O

*Remarks.* A single encrinurid pygidium, which is incomplete posteriorly, differs from the others known from the Poley Cow Formation. The specimen resembles pygidia of *Batocara fritillum* in overall proportions but has a wider and more strongly tapering axis, fewer axial rings and pleural ribs, ring furrows containing elliptical apodemal pits laterally, and wider (exsag.) inter-rib furrows.

**Calymenidae** Milne Edwards, 1840

**Flexicalymeninae** Siveter, 1977

(= Metacalymeninae Přibyl and Vaněk, 1977)

*Remarks.* Flexicalymeninae and Metacalymeninae are considered here to be synonymous. Although Přibyl and Vaněk's publication establishing Metacalymeninae is dated 1975, the date of issue given inside the front cover of the volume is December 1977. Dr Siveter has informed me that his publication was issued in April 1977. Flexicalymeninae thus has priority over Metacalymeninae.

***Gravicalymene*** Shirley, 1936

*Type species. Gravicalymene convolva* Shirley, 1936, from the lower Ashgill of south Wales; original designation.

*Remarks.* The following species belongs to the group for which Chatterton and Campbell (1980) proposed the genus *Apocalymene*. The difficulty of classifying such species was discussed by Holloway (1980), who concluded that present knowledge of calymenid relationships does not enable the discrimination of *Apocalymene* from *Sthenarocalymene* Siveter, 1977. *Sthenarocalymene* was considered by Siveter (1977) and Holloway (1980) to differ from *Gravicalymene* in the form of the anterior cephalic border. Price (1982), however, presented evidence that the form of the anterior border is too variable to be used to distinguish between these two genera, lending support to doubts raised by other workers (e.g., see Price, 1982: 58) on the taxonomic usefulness of this character at the generic level. Price therefore placed *Sthenarocalymene* in synonymy with *Gravicalymene*. Until the relationships of calymenids of *Apocalymene* and *Sthenarocalymene* type are clarified, I prefer to assign such species to *Gravicalymene* with question.

***Gravicalymene*? *vaccina*** sp. nov.

Figure 9

*Etymology.* Latin *vaccinus*, of cows, referring to the Poley Cow Formation.

*Type material.* Holotype: cranidium NMV P138830A, B (counterparts), Fig. 9A, B.

Paratypes: NMV P138831–P138838 (cranidia); NMV P134883, P138839–P138842 (librigenae); NMV P134867, P138843–P138847 (hypostomes); NMV P138848–P138856 (pygidia).

*Diagnosis.* Anterior cephalic border as long (sag.) as occipital ring, gently upturned. L1 large, almost as wide as adjacent median part of glabella, with anterior edge opposite glabellar midlength. Midlength of palpebral lobe opposite S2 or slightly farther forward. Hypostome with broad posterior border spines having abaxial and adaxial margins convex in outline, separated by sharp notch. Pygidium with narrow, gently taping axis of 6–7 rings, 5 sharply impressed pleural furrows, and no vincular furrow.

*Description.* Glabella bell-shaped, widest towards back of L1 and approximately 0.6 times as wide across frontal lobe; front of glabella flattened in outline medially, level with front of fixigenal field or projecting slightly farther forwards. Occipital ring decreasing in length abaxially behind L1, flexed forwards slightly distally; occipital furrow increasing greatly in depth behind L1. L1 ovate; posterior branch of S1 shallowing abruptly opposite middle (exsag.) of L1 but extending to occipital furrow. L2 subcircular or elliptical, half as long (exsag.) as L1 and not as distinctly separated from median part of glabella. L3 nodular, half as long (exsag.) as L2; S3 narrow (tr.), shallow and situated at 0.25 times glabellar length. Axial furrow containing anterior pit just behind anterolateral extremity of frontal lobe; preglabellar furrow not as deep as axial furrow but recessed slightly beneath front of glabella. Anterior border flattened (sag., exsag.) behind strongly rounded crest; anterior border furrow shallow and well-rounded in cross section. Fixigenal field convex (exsag.), sloping steeply forwards in front of palpebral lobe; anterior edge of palpebral lobe opposite S3, pos-

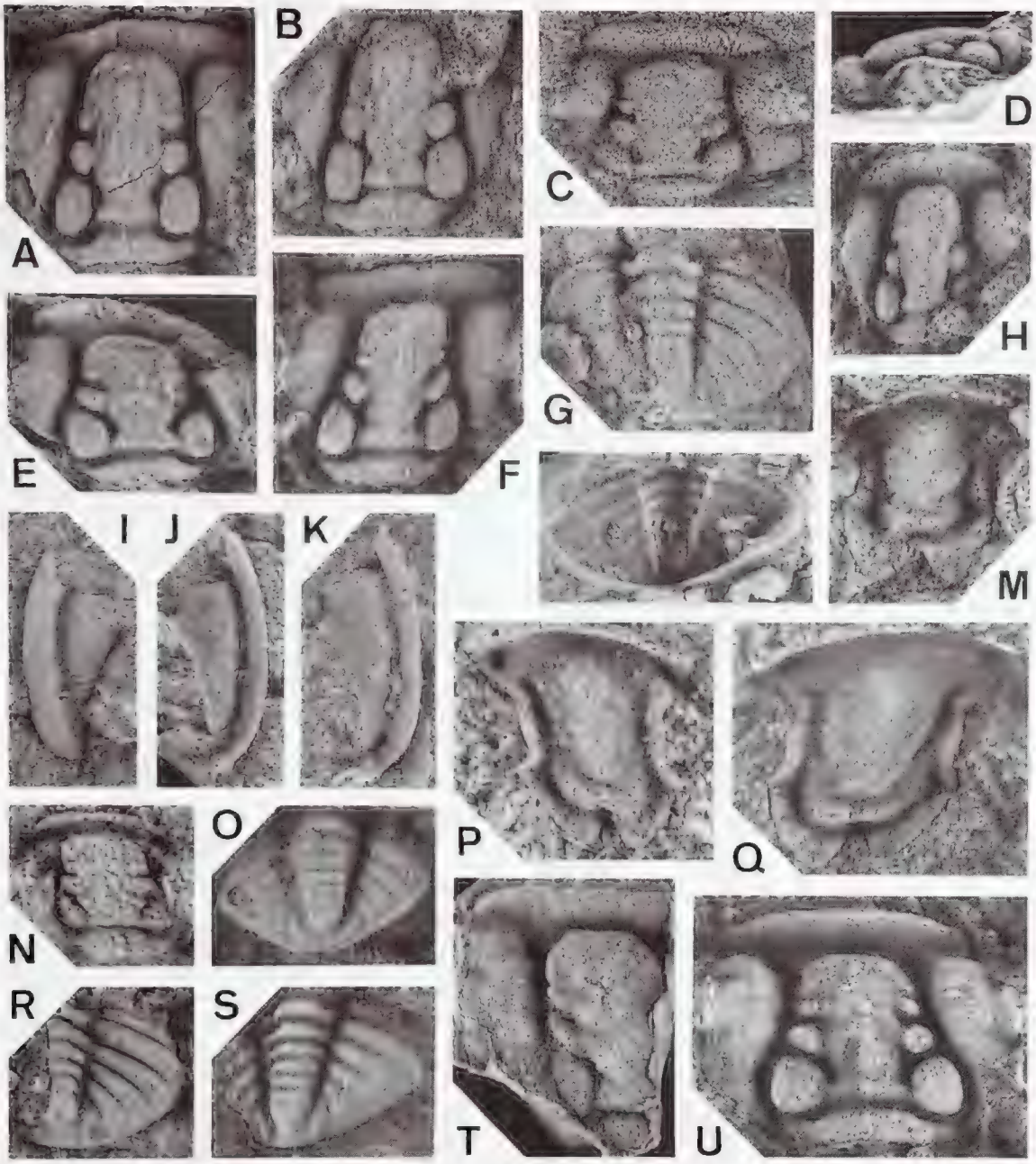



Figure 9. *Gravicalymene? vaccina* sp. nov. A, B, holotype, cranidium NMV P138830, internal mould and latex cast of external mould, dorsal views, × 3.5. C, cranidium NMV P138831, latex cast of external mould, dorsal view, × 5. D, H, cranidium NMV P138832, latex cast of external mould, lateral and dorsal views, × 5. E, cranidium NMV P138833, internal mould, dorsal view, × 5. F, cranidium NMV P138834, internal mould, dorsal view, × 5. G, pygidium NMV P138848, latex cast of external mould, dorsal view, × 3. I, J, left librigena NMV P138839, latex casts of counterpart moulds, dorsal and ventral views, × 3.5. K, left librigena NMV P138840, latex cast of natural mould, ventral view, × 3.5. L, pygidium NMV P138849, latex cast of natural mould, ventral view, × 3.5. M, hypostome NMV P134867, latex cast of external mould, ventral view, × 8. N, cranidium NMV P138835, internal mould, dorsal view, × 10. O, pygidium NMV P138850, internal mould, dorsal view, × 6. P, hypostome NMV P138843, latex cast of external mould, ventral view, × 7. Q, hypostome NMV P138844, internal mould, ventral view, × 7.5. R, pygidium NMV P138851, latex cast of external mould, dorsal view, × 3. S, pygidium NMV P138852, internal mould, dorsal view, × 3. T, cranidium NMV P138836, latex cast of external mould, dorsal view, × 4. U, cranidium NMV P138837, internal mould, dorsal view, × 4.5.

terior edge opposite outer end of S1. Anterior branch of facial suture mostly subparallel to sagittal line or converging weakly, curving strongly inwards across front of anterior border furrow; posterior branch of suture (interpreted from librigena) directed laterally or even slightly forwards from ε, flexed more strongly backwards about half way to lateral border furrow. Librigena with gently convex field, shallow lateral border furrow, and broad and well-rounded border; doublure flattened, inner edge lying close beneath inner part of border.

Hypostome approximately as wide across shoulders as long (sag.), about 1.5 times wider across anterior wings; anterior margin broadly rounded, lateral margin subparallel between anterior wing and shoulder; notch between posterior spines extending forwards to posterior border furrow. Anterior lobe of middle body elliptical, rising steeply to a central prominence; posterior lobe crescentic, slightly inflated, wider (tr.) than anterior lobe; middle furrow deepest abaxially and medially, median part lying opposite shoulder; maculae inconspicuous. Anterior border flexed ventrally to form a sharp flange separated from middle body by a long (sag., exsag.), poorly delimited depression; anterior wing with deep pit. Lateral border strongly convex (tr.), of uniform width except towards shoulder where it expands slightly; lateral border furrow firmly impressed. Posterior spines flattened; posterior border furrow increasing in depth abaxially and medially.

Pygidium 1.5–1.6 times as wide as long, lenticular to rhombic in outline. First axial ring flexed slightly forwards distally and with weak node; rings 2 and 3 with pseudo-articulating half rings medially; all except last ring furrow deepest abaxially. Axial furrow very shallow behind axis. Pleural lobes gently convex (tr.); posterior margin arched upwards towards sagittal line. Pleural furrows shallowing abaxially but distinguishable almost to margin; interpleural furrows weak, most distinct abaxially; posterior pleural band on fifth segment depressed abaxially, bounding gently convex (tr.) postaxial region. Doublure narrow and sharply rounded in cross section.

External surface of cranidium, librigena, hypostome and pygidium with traces of granulose sculpture.

*Remarks.* The preserved shape of the glabella of *Gravicalymene*? *vaccina* and the degree to which the anterior border is upturned vary due to deformation of the specimens (e.g., compare Fig. 9A, C, H). The holotype (Fig. 9A, B) appears to be the least deformed specimen. A very small cranidium (Fig. 9N), 1.9 mm in length, differs from larger cranidia in having a broader, more subquadrate glabella and a shorter (sag.), sharply upturned anterior border, although these differences could again be due to deformation. L1 is subtriangular; S1 is rather shallow at the axial furrow, the anterior branch is very weak and transverse, and the posterior branch is deep but dies out abruptly just in front of the occipital furrow. S2 and S3 are transverse and narrow, S3 being very shallow; L2 is not separated from the median part of the glabella. The cranidium is rather coarsely granulose and there is a median tubercle on the occipital ring.

*Gravicalymene*? *vaccina* is very similar to *G*? *hetera* Gill, 1945 and *G*? *kilmorensis* Gill, 1945, both from the Ludlow of central Victoria, and *G*? *coppinsensis* (Chatterton and Campbell, 1980) from the Wenlock of the Australian Capital Territory. *G*? *hetera* and *G*? *kilmorensis*, which are probably synonymous (Holloway and Neil, 1982), differ from *G*? *vaccina* in having a more upturned anterior cephalic border and slightly more posteriorly placed palpebral lobes, with their midlength opposite L2 rather than S2. *G*? *coppinsensis* has a smaller L1 than *G*? *vaccina*, slightly narrower posterior hypostomal spines separated by a broader median notch, a more strongly tapering pygidial axis, less sharply impressed pygidial pleural furrows (except the first), and interpleural furrows that are more distinct abaxially. *G*? *cootamundrensis* (Gill, 1940), from strata in New South Wales previously assigned a Late Silurian age but now known to be Early Devonian (Adrian, 1978), is also similar to *G*? *vaccina* but has a slightly more upturned anterior border, a somewhat smaller L1, coarser cranidial granulation, and pygidial pleural and interpleural furrows that are deeper abaxially.

*Gravicalymene*? *changyangensis* (Chang, 1974) from the Silurian of south-west China is distinguished from *G*? *vaccina* by its less bell-shaped glabella with much smaller L1.

The incomplete calymenid pygidium figured by Lane and Thomas (1978, pl. 2, fig. o), from the Quinton Formation in the Grey Creek area of the Broken River Province, differs from pygidia of *Gravicalymene*? *vaccina* in having longer (exsag.) pleural furrows that curve more strongly backwards abaxially and extend closer to the pygidial margin, and interpleural furrows that are deeper abaxially.

**Odontopleuridae** Burmeister, 1843

**Odontopleurinae** Burmeister, 1843

*Remarks.* A number of odontopleurid genera were assigned by Ramsköld and Chatterton (1991) to the Acidaspidinae Salter, 1864, a subfamily previously considered synonymous with the Odontopleurinae. Ramsköld and Chatterton stated that their concept of the Acidaspidinae is new but did not give a full diagnosis as details are to be presented elsewhere. Pending the publication of these details, the Acidaspidinae is not recognised here.

***Gaotania*** Chang, 1974

*Type species. Gaotania ovata* Chang, 1974, from the upper Llandovery of south-west China; original designation.

*Remarks. Gaotania* is not well known, morphological information on the genus having been derived mostly from the cephalon and pygidium of the type species illustrated by Chang (1974, pl. 82, figs 7, 8). Another Chinese species, *G. pulchella* Chang, 1974, is based on a very poorly preserved dorsal exoskeleton, and has also been recorded from poorly preserved material by Wu (1977: 103, pl. 2, figs 15, 16; note that the numbering of figs 12 and 16 is transposed on Wu's plate 2). Poorly preserved specimens assigned to *G. ovata* by Chang and Meng (1986: 513, pl. 3, figs 8–12) apparently do not belong to that species, as the major border spines on the pygidium are not greatly inflated.

Ramsköld and Chatterton (1991) considered *Gaotania* to belong to a monophyletic group of genera that also includes *Globulaspis* Reed, 1931, *Stelckaspis* Chatterton and Perry, 1983 and *Uriarra* Chatterton and Campbell, 1980. *Gaotania* is extremely similar to *Stelckaspis* and was considered to be a senior synonym of that genus by Lane (1988). Characters shared by the two genera include: glabella narrower than the cheeks; frontal lobe not expanded laterally; L3 absent; L2 weakly separated from the median lobe; facial suture apparently fused in holaspides; eyes situated posteriorly and very close to the glabella; anterior and lateral cephalic border furrows joining in a curve; genal spines relatively short and stout; and pygidium with two pairs of median secondary border spines between the major spines. Ramsköld and Chatterton (1991: 356) stated that the pygidium of *Gaotania* differs from that of *Stelckaspis* in having the lateral pair of median secondary border spines partly fused with the major spine pair instead of being separate. Partial fusion of these spines is, however, variably developed within some other odontopleurid genera; among species assigned by Ramsköld and Chatterton to *Meadowtownella*, these spines are partly fused in *Primaspis ascita* Whittington (1956: 199, pls 1, 2) and *Acidaspis trentonensis* Hall (see Ross, 1979: D8, pl. 4, figs 8–11) but not in *Acidaspis girvanensis* Reed (1914: 33, pl. 5, figs 8–10, pl. 6, figs 1–3). This suggests that partial fusion of pygidial spines may develop independently within lineages and should be used with caution in adducing relationships. Species assigned to *Gaotania* also differ from those assigned to *Stelckaspis* in that the occipital lobes are very weak or absent and the pygidial pleural ridge is more poorly defined along its adaxial edge.

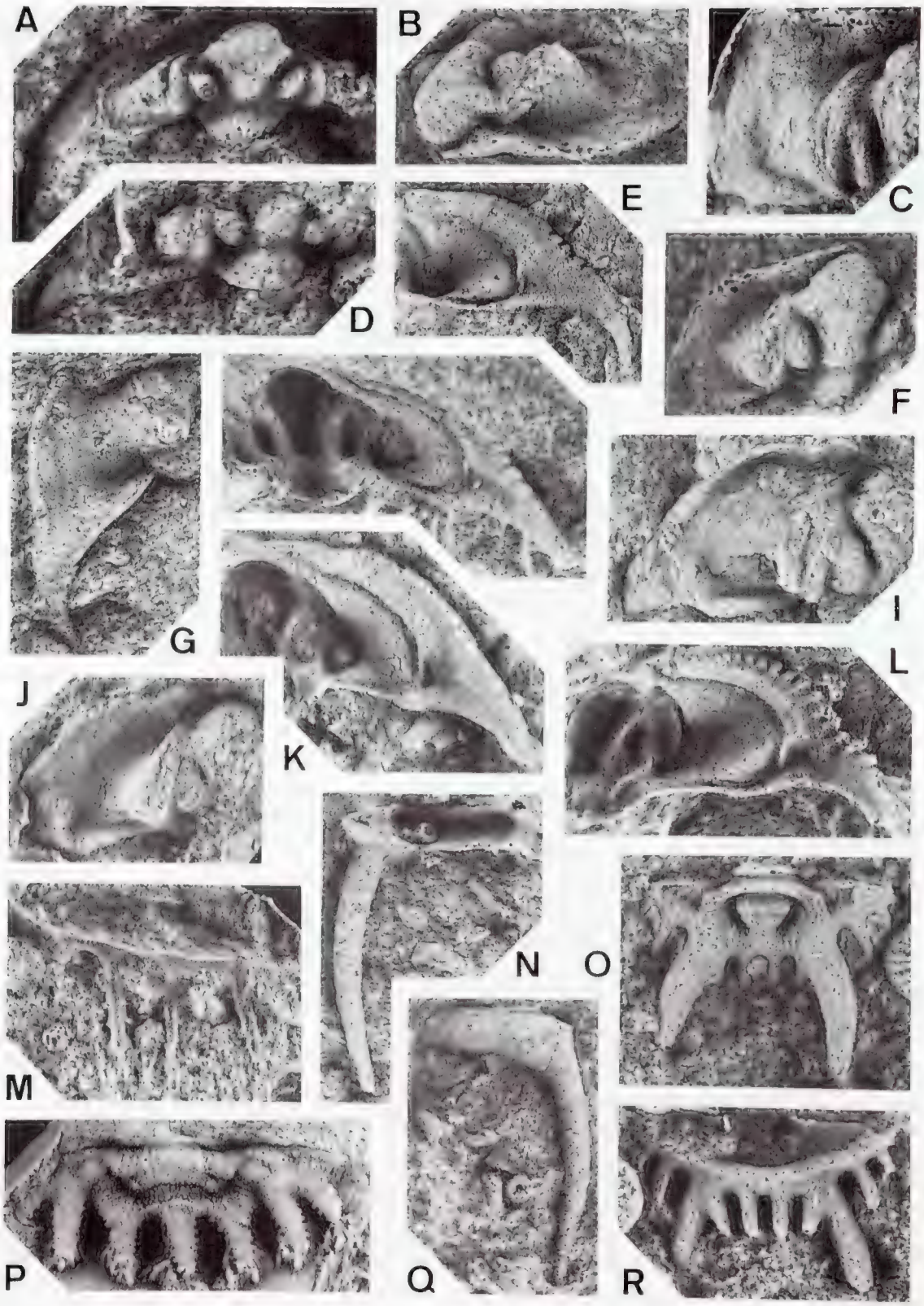
*Globulaspis* is even more poorly known than *Gaotania*, the type and only known species, *Globulaspis prominens* (Reed, 1931) from the lower Llandovery of Scotland, being represented only by several fragmentary cranidia (Howells, 1982, pl. 15, figs 8, 12, 13). The narrow frontal lobe, the absence of L3, the relatively weak isolation of S2 from the median glabellar lobe and the narrow, rather inflated part of the fixigena adaxial to the palpebral lobe and eye ridge are similarities with *Gaotania* and *Stelckaspis*, and the apparent absence of occipital lobes suggests a greater similarity with the former. *G. prominens* differs from species assigned to both *Gaotania* and *Stelckaspis* in having a functional facial suture. *Globulaspis* may eventually be judged to be a senior synonym of one or both of these genera, but until the discovery of more complete material of *G. prominens*, including pygidia, I consider that *Globulaspis* should be restricted to that species.

*Uriarra*, known only from the type species *U. kausi* Chatterton and Campbell, 1980 from the Wenlock of the Australian Capital Territory, resembles *Stelckaspis* and *Gaotania* in most of the cephalic characters shared by those genera but differs in having S2 strongly separated from the median glabellar lobe, a longer (sag.) occipital furrow, secondary spines along the dorsal edge of the genal spine and a pygidium with only one pair of median secondary border spines between the major spines.

***Gaotania bimusa*** sp. nov.

Figure 10A–M, N, O, Q, R

*Etymology.* Latin *bi-*, two, together with the generic name of the banana, in reference to the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major border spines on the pygidium. Noun in apposition.

*Type material.* Holotype: pygidium NMV P138857A, B (counterparts), Fig. 10O, R.

Paratypes: NMV P134837, P138858–P138868 (cephala); NMV P138869, P138870 (thoracic segments); NMV P134807, P138871 (pygidia).

*Diagnosis.* Pygidium with inflated major border spines having distinct backward flexure at mid-length, and with two pairs of secondary border spines lateral to major spines.

*Description.* Cephalon including genal spines crescentic in dorsal view; anterior margin apparently flexed forward slightly directly in front of eye, more or less transverse in outline medially (Fig. 10K). Glabella expanding slightly from occipital ring almost to front of L1, thereafter narrowing strongly. Occipital ring strongly arched (tr.), decreasing greatly in length abaxially behind L1; occipital furrow long (sag., exsag.) and shallow medially, deeper and more sharply impressed laterally. L1 elliptical to ovate, separated from median lobe by deep, oblique S1 and less-sharply impressed longitudinal furrow. L2 much smaller than L1, not separated from median lobe; S2 notching side of glabella. Axial furrow deep alongside posterior part of L1 and in front of S2, shallow elsewhere. Eye situated opposite L1, together with arcuate eye ridge isolating a narrow, inflated sliver of cheek adjacent to axial furrow; lateral and anterolateral to eye and eye ridge, cheek gently concave (tr.) and inclined. Lateral border flattened or weakly concave (Fig. 10B), very wide posteriorly and narrowing strongly forwards; lateral border furrow shallow. Genal spine broad proximally and tapering strongly distally. Cephalic margin with at least 16 blunt, downwardly-directed spines in a row extending from more or less directly in front of eye onto base of genal spine. Cephalic doublure with deep, exsagittally elongated depression situated adjacent to inner margin at base of genal spine (Fig. 10K).

Thoracic segments with long (exsag.), convex pleural ridge and very short (exsag.) anterior articulating flange abaxially (Fig. 10N, Q); anterior pleural spine short, blunt and downwardly directed; posterior spine long, stout and gently curved.

Pygidium excluding border spines approximately 2.7 times as wide as long. Axis with width across articulating half ring approximately 0.25 times maximum pygidial width, slightly narrower across second axial ring but much wider across first ring. First axial ring highly elevated and gently arched forwards; second ring much lower, weakly separated from terminal piece of axis, with a short (sag.), steeply inclined pseudo-articulating half ring lying beneath posterior edge of first ring and separated from remainder of second ring by a deep furrow. Axial furrow very deep lateral to second ring and terminal piece of axis, not impressed adjacent to first ring or behind axis. Pleural lobe with slightly raised anterior margin and broad, gently convex border that slopes backwards between major border spines. Pleural ridge short, extending obliquely backwards from first axial ring and merging with border in front of lateral part of major spine base. Major spines extending backwards more than twice sagittal length of pygidium; first (most anterior) secondary spine smaller than second, both curving backwards abaxially subparallel to proximal part of major spine but directed more ventrally than it; third and fourth secondary spines similar in size to second, directed posteroventrally, third spines converging slightly backwards, fourth spines subparallel (Fig. 10O). Doublure divided into inner and outer bands by an angular, transverse ridge; inner band expanding adaxially to a point in front of major spine base and thereafter increasing in slope.

Exterior of cephalon and pygidium with granulose sculpture.

*Remarks. Gaotania bimusa* is more closely related to *G. ovata* than to *G. pulchella*. Charac-

Figure 10. A–M, N, O, Q, R, *Gaotania bimusa* sp. nov. A, D, cephalon NMV P138858, internal mould and latex cast of external mould, dorsal view, × 8.5. B, F, H, cephalon NMV P138859, latex casts of counterpart moulds, oblique, dorsal and ventral views, × 8. C, cephalon NMV P138860, latex cast of external mould, dorsal view, × 7.5. E, cephalon NMV P138861, latex cast of natural mould, ventral view, × 5. G, cephalon NMV P138862, latex cast of external mould, dorsal view, × 5. I, cephalon NMV P138863, latex cast of external mould, dorsal view, × 7. J, cephalon NMV P138864, latex cast of external mould, dorsal view, × 7. K, cephalon NMV P138865, latex cast of natural mould, ventral view, × 6. L, cephalon NMV P138866, latex cast of natural mould, ventral view, × 5. N, Q, thoracic segment NMV P138869, latex casts of counterpart moulds, ventral and dorsal views, × 5. O, R, holotype, pygidium NMV P138857, latex casts of counterpart moulds, dorsal and ventral views, × 8. M, P, *Ceratocephala* sp. M, pygidium NMV P138872, latex cast of natural mould, ventral view, × 5. P, pygidium NMV P138873, latex cast of external mould, dorsal view, × 3.

ters in which the first two species differ from the last are the inflated major border spines on the pygidium, the secondary border spines that are much smaller than the major spines, and the distinct pygidial border abaxial to the major spines. The pygidium of *G. bimusa* differs from that of *G. ovata* in having only one secondary border spine lateral to the major spine rather than two, the major spine is not as distinctly flexed backwards at midlength, the posterior pair of secondary spines diverge backwards instead of being subparallel, and the pygidial granulation is apparently coarser. *G. bimusa* seems to have shorter, more strongly tapering genal spines than either of the Chinese species, but cephala of all three species are too poorly preserved for further useful comparison.

**Ceratocephalinae** Richter and Richter, 1925

***Ceratocephala*** Warder, 1838

*Type species. Ceratocephala goniata* Warder, 1838, from the Silurian of Ohio; by monotypy.

***Ceratocephala*** sp.

Figure 10M, P

*Remarks.* The more complete of two pygidia belonging to this genus lacks the left lateral extremity and the distal parts of the marginal spines (Fig. 10P). The specimen seems to have been deformed by upward flexing of the anterior portion along a transverse line passing between the second and third marginal spines. As a result, the axis appears to slope very steeply backwards with respect to the remainder of the pygidium.

*Ceratocephala* species with three, seven or nine marginal spines on the pygidium are known from the Silurian. In having seven spines and two axial rings, the present specimens most closely resemble *C. plummeri* Chatterton and Perry, 1983 from the lower Wenlock of Canada, but the first and second marginal spines are more laterally directed than in that species, the barbs on the marginal spines are finer (to judge from their broken bases), the exoskeletal granulation is less uniform in size, and there is a pair of small tubercles on the first axial ring. The second ring furrow appears to be much deeper and the terminal piece of the axis more depressed in the present material, but these differences can be attributed to deformation. Other Silurian species of *Ceratocephala* with seven pygidial marginal spines are *C. rhabdophora* (Hawle and Corda, 1847) (redescribed by Šnajdr, 1986) from the upper Ludlow to lowermost Přídolí of Bohemia, *C. vogdesi* Etheridge and Mitchell, 1897 from the upper Ludlow of the Yass Basin, New South Wales, and *Ceratocephala* n. sp. A of Chatterton and Campbell, 1980 from the Wenlock of Canberra. Pygidia of these species differ from the present specimen in having only one axial ring.

"*Ceratocephala*" *impedita* Etheridge and Mitchell, 1897, based on cranidia from the Ludlow of the Yass Basin and revised by Chatterton (1971), actually belongs to *Miraspis*, as shown by the S1 that is directed obliquely backwards from the longitudinal furrow instead of obliquely forwards, and the median glabellar lobe that is widest at the inner end of S1 instead of narrowing forwards from the occipital furrow.

**Acknowledgements**

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# PHYLOGENY AND BIOGEOGRAPHY OF THE GNATHIIDAE (CRUSTACEA: ISOPODA) WITH DESCRIPTIONS OF NEW GENERA AND SPECIES, MOST FROM SOUTH-EASTERN AUSTRALIA

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## Abstract

Cohen, B.F. and Poore, G.C.B., 1994. Phylogeny and biogeography of the Gnathiidae (Crustacea: Isopoda) with descriptions of new genera and species, most from south-eastern Australia. *Memoirs of the Museum of Victoria* 54 (2): 271–397

The classification of the Gnathiidae is reviewed for the first time since Monod (1926). States of 72 characters are discussed with reference to two outgroups of Flabellifera, forming the basis of a phylogenetic analysis. Ninety-five species are included in the analysis representing all nominal genera and subgenera and covering the perceived variation in the family. Results indicate that the Gnathiidae can be divided into two principal clades representing one (*Thaumastognathia* Monod) and nine genera (*Gibbagnathia* gen. nov., *Paragnathia* Omer-Cooper and Omer-Cooper, *Euneognathia* Stebbing, *Bythognathia* Camp, *Monodgnathia* gen. nov., *Bathygnathia* Dollfus, *Caecognathia* Dollfus, *Gnathia* Leach and *Elaphognathia* Monod).

The new classification differs from that of Monod (1926) in the description of two new genera (*Monodgnathia* and *Gibbagnathia*), the revival of another genus previously in synonymy (*Caecognathia*), the elevation of a subgenus to generic rank (*Elaphognathia*) and the loss of two genera and a subgenus in synonymy (*Heterognathia*, *Akidognathia* and *Perignathia*). The elevation of *Elaphognathia* to generic rank relies on the recognition of paraphyletic *Gnathia*. A key to the proposed genera of Gnathiidae is presented.

Twenty-five new species are described and figured from south-eastern Australia, three from deep water in the Tasman and Coral Seas, and one from New Zealand. *Thaumastognathia* is recorded for the first time since 1926. *Bathygnathia*, *Monodgnathia*, and *Thaumastognathia* are recorded for the first time from Australian waters. Keys to all 45 Australian species are offered with figures of the cephalosomes of the 17 previously described species to aid identification. Habitat and distributional data for all Australian species are presented.

The phylogenetic analysis of the family suggests the most significant evolutionary events in the radiation of the family took place in the cold waters of the southern hemisphere. *Thaumastognathia*, sister group of all other gnathiids, is an endemic genus of four species from the Australian-New Zealand shelf. *Gibbagnathia*, the second clade, is an endemic, monotypic genus confined to Bass Strait, southern Australia. *Paragnathia* is enigmatic in being a single Afro-European species but *Euneognathia* is a single species from the Antarctic shelf. None of these four genera has radiated successfully. *Bythognathia* (1 species) is from the deep sea (4000 m) of the Caribbean. *Monodgnathia* (4 species) and *Bathognathia* (12 species) are both confined to the slope and deep sea. But radiation has been moderate and with the exception of the one species of *Bythognathia* none is found very deep, unlike many other families of isopods.

Two related clades have radiated strongly in more shallow and warmer waters: *Caecognathia* with 43 species distributed more towards the poles than *Gnathia-Elaphognathia* (89 species.) which is more cosmopolitan on temperate and tropical shelves and upper slopes. Small clades of species of *Caecognathia* are confined to Australia. Other species of the highly endemic southern Australian fauna seem to have arisen locally and independently.

## Table of Contents

## Introduction

The waters around Australia possess a rich crustacean fauna (Barnard, 1991; Poore et al., 1994), best documented in the south-eastern temperate region where extensive recent research has been completed. The isopod family Gnathiidae is one of many contributing to this diversity but contains numerous undescribed species.

Gnathiids are most unusual isopods, polymorphic in the extreme. Males are immediately recognisable by their large forwardly-directed mandibles and five pairs of walking legs. Females have more reduced jaws and a thorax swollen with ovary or eggs. The juveniles, or praniza larvae, pass through three instars in the only species studied (Wägele, 1987, 1988), each feeding on blood as ectoparasites of fishes. The praniza appears like a thinner female, also with five pairs of legs and sometimes with guts engorged with blood.

The morphology and classification of the Gnathiidae was placed on an excellent footing by Théodore Monod. Monod's (1926) volume described in detail the anatomy and biology of the group and illustrated the 62 species then known. Camp (1988) listed a further 42 species described since Monod's (1926) work. Eighteen species have been described since Camp's work, two were overlooked by him (Table 1), and a further 29 are described here. This brings the total number of described species of Gnathiidae to 155. There has been no reappraisal of the relationship of the genera since that by Monod (1926).

Prior to this study 17 species of Gnathiidae were known from Australia, only six from the temperate waters of the south-east. Holdich and Harrison (1980) suggested that poor sampling effort, rather than low species diversity, was responsible for the low number of Australian species and that further sampling should uncover more species. This has proved true. This paper addresses the fauna of south-eastern Australia, from near Nowra, New South Wales (35°S, 150°E) around Tasmania (43°S) and across to Pearson Island (34°S, 134°E) west of the Spencer Gulf, South Australia. It describes four times as many species as were previously known from this region, recognises two new genera, is the first record of *Thaumastognathia* in over 65 years, the first records of *Bathygnathia* and *Thaumastognathia* from Australia and the first records of gnathiids from Tasmanian waters. Four significant Australasian species from outside this region are also described, all from deep water. It is now apparent that Australia possesses a rich gnathiid fauna with approximately one-quarter of all the species so far described.

New species are described and figured. Most species previously described from Australia were well illustrated and described by Monod or later authors. Figures of their cephalosomes (Fig. 2) have been copied to aid in identification when using the keys.

As well as describing numerous new species from Australian coastal, shelf and slope environments we present a new phylogeny and classification of the family. This phylogeny is based on a cladistic analysis of 95 described species from world-wide localities. On the basis of this analysis two new genera are described, one is revived, a subgenus is elevated to generic rank, and other genera are lost in synonymy. A key to the ten

Table 1. Gnathiidae described since 1987 (including two overlooked by Camp, 1988). Species have been reallocated to genus according to the classification scheme adopted in this paper. Each species is followed by its type locality, depth of capture and size of male, when available. Species described prior to this date were listed by Monod (1926) and supplemented by Camp (1988). Coordinates of type localities are those listed by original authors; where size was not stated it was measured from figures.

*Bythognathia yucatanensis* Camp, 1988: Yucatan Channel, Caribbean Sea, 21°07.0′–13.0′N, 85°31.5′–32.0′W; 3700–3800 m; 20.8 mm.
*Caecognathia amakusaensis* (Nunomura, 1992): Use, Reihoku-cho, Kumamoto Pref., Japan; 30–35 m; 5.1 mm.
*Caecognathia kikuchii* (Nunomura, 1992): Shiraiwazaki, Reihoku-cho, Kumamoto Pref., Japan; 3.7 mm.
*Caecognathia saikaiensis* (Nunomura, 1992): off Tomoezaki, Japan; 3.1 mm.
*Elaphognathia cornigera* (Nunomura, 1992): Tûjishima Islet, Itsuwa-chô, Kumamoto Pref., Japan; 2.4 mm.
*Elaphognathia discolor* (Nunomura, 1988): Isohara, Kita-ibaragi shi, Ibaragi, Central Japan; 6.2 mm.
*Elaphognathia wolffi* (Müller, 1989a): Coral Reef near Tiwi, Mombasa, Kenya; 1.6 mm.
*Gnathia calsi* Müller, 1993b: La Trinité, Anse Rivière, Martinique, French Antilles; 0–2 m; 1.9 mm.
*Gnathia cooki* Müller, 1989c: Cooks Bay, Moorea, Society Is; 1 m; 3.7 mm.
*Gnathia firingae* Müller, 1991: La Réunion L'Ermitage-les-Bains; 0.5–1 m; 2.1 mm.
*Gnathia galzini* Müller, 1989c: Moorea, Society Is; 0.5 m; 1.6 mm.
*Gnathia gonalezi* Müller, 1988: Punta de Betin, Sta Marta, Colombia; 15 m; about 1.5 mm.
*Gnathia hirayamai* Nunomura, 1992: Tomioka, Amakusa, Kumamoto Pref., Japan; 8.5 m; 3.9 mm.
*Gnathia incana* Menzies and George, 1972: Peru-Chile Trench, 11°50′S, 77°58′W; 935–907 m; 3.6 mm.
*Gnathia lacunacapitalis* Menzies and George, 1972: Peru-Chile Trench, 07°59′S, 80°37′W; 991–1015 m; 4.5 mm.
*Gnathia lignophila* Müller, 1993a: Pulau Babi Besar, Tioman Archipelago, Malaysia; lower-intertidal; 1.9–2.9 mm.
*Gnathia magdalenensis* Müller, 1988: Bahía de Nenguangue, Colombia; 18 m; about 2.7 mm.
*Gnathia malaysiensis* Müller, 1993a: Pulau Babi Besar, Tioman Archipelago, Malaysia; 1–2 m; 2.3 mm.
*Gnathia nasuta* Nunomura, 1992: off Tomoezaki, Kumamoto Pref., Japan; 8.5 m; 3.3 mm.
*Gnathia nicembola* Müller, 1989b: Entrance channel to Suva Harbour, Fiji; 76–84 m; 2.6 mm.
*Gnathia samariensis* Müller, 1988: Isla de Morro Grande, Colombia; 30 m; about 1.95 mm.
*Gnathia vellosa* Müller, 1988: Isla de Morro Grande, Colombia; 25–30 m; about 1.2 mm (excluding pleon).

world genera now recognised and a checklist of species in the new classification are presented. Updated keys to the species of Australia are offered.

## Materials

Much of the material on which this study is based has come from large benthic surveys of the bays, shelf and slope of southern and eastern Australia:

Crib Point Benthic Survey, 1965–1972 (CPBS) carried out in Western Port, Victoria, by the Marine Studies Group, Ministry for Conservation, Melbourne;

Bass Strait Survey, 1979–1985 (BSS) carried out by the Museum of Victoria, Melbourne (see Wilson and Poore, 1987 for station locations and methods);

south-eastern Australian slope study, 1986, 1988 carried out by the Museum of Victoria, Melbourne (see Poore et al., 1994, for station locations, methods and a discussion of the diversity of Isopoda);

the 1986 *Cidaris* cruise in the western Coral

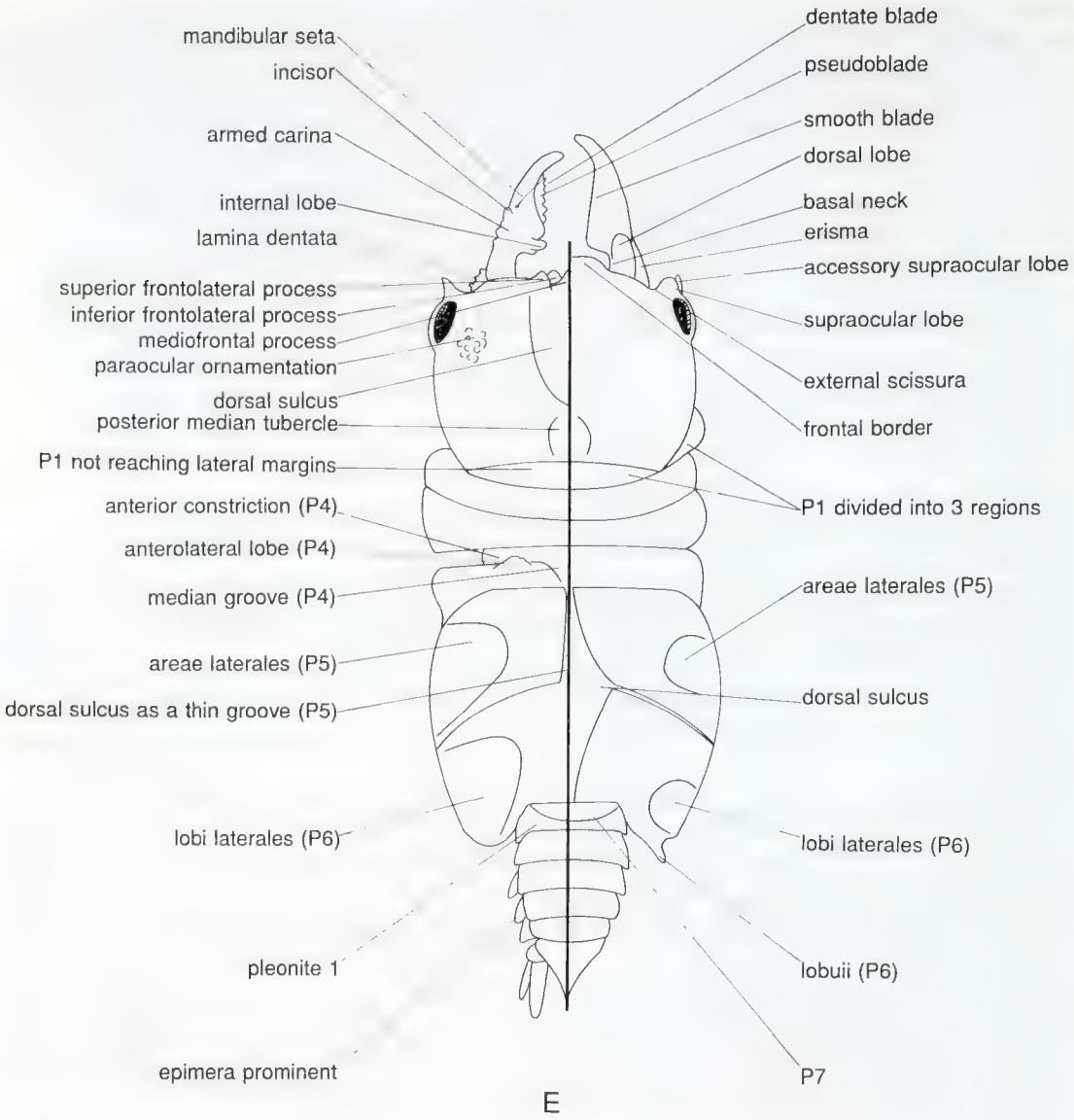



Figure 1. Stylised male gnathiid (dorsal view) showing main anatomical features.

Sea, carried out by James Cook University of North Queensland; and

other material from the collections of the Australian Museum, Sydney and the Museum of Victoria, Melbourne.

All type material is lodged in the collections of the Museum of Victoria, Melbourne (NMV), Australian Museum, Sydney (AM), Queensland Museum, Brisbane (QM) and New Zealand Oceanographic Institute, Wellington (NZOI).

Only males were described because of the difficulty of identifying praniza stages and females. In the species-rich environment of south-eastern Australia, dredge samples with more than one species of gnathiid were common, therefore association of females and pranizas with males was not considered a sufficient criterion for identification. No obvious characters were found that enabled females or pranizas to be accurately identified to species and this problem

was not explored. Identification of females and pranizas to the species level would be a major project and was not attempted here.

We follow the anatomical terminology used by Monod (1926) and Holdich and Harrison (1980) except for numbering of pereonites and pereopods (Fig. 1). The first body segment posterior to the cephalon, pereonite 1 (correctly thoracomere 2, not pereonite 2 as in Monod's and Holdich and Harrison's works), is fused to the cephalon forming a cephalosome. In some species pereonite 1 may be dorsally indistinguishable from the cephalon. The pylopod (pereopod 1) attaches to pereonite 1. Pereonites 2–6 follow posteriorly with pereonite 2 possessing the most anterior of the five pairs of walking legs. The pereopods are labelled according to the pereonite to which they are attached (pereopods 2–6). Pereonite 7, when distinguishable, is very small and functionally forms part of the outline of the pleon.

The scale bar is 1 mm and refers only to drawings of whole animals in dorsal view. Figure labels are as follows: A1, A2, antenna 1 and 2; PY, pylopod (pereopod 1); MP, maxilliped; P2–P6, pereopods 2–6 (walking legs 1 to 5); U, uropods; l, r, left and right. All illustrations are of the male holotype unless otherwise stated. Figure 1 is of a stylised male gnathiid and is labelled to show parts of the animal and its ornamentation.

Monod's (1926) review of the Gnathiidae was extremely detailed and included over 300 references. His synonymies were detailed, therefore, they are not repeated here in full. Hesse (1864) highlighted the similarity of gnathiids to ants (Formicidae) with the specific name *Anceus formica*. The specific epithets of new species here described are genera of Australasian ants (Taylor, 1987) chosen only for their euphony, not to reflect any specific feature of either the isopod or the ant. All are nouns in apposition.

Morphological characters were coded into the taxonomic database program DELTA (Dallwitz and Paine, 1986) for all Australian species. Descriptions were generated from this program but were heavily edited. The database is available on request by DELTA users from the Department of Crustacea.

## Phylogenetic methods

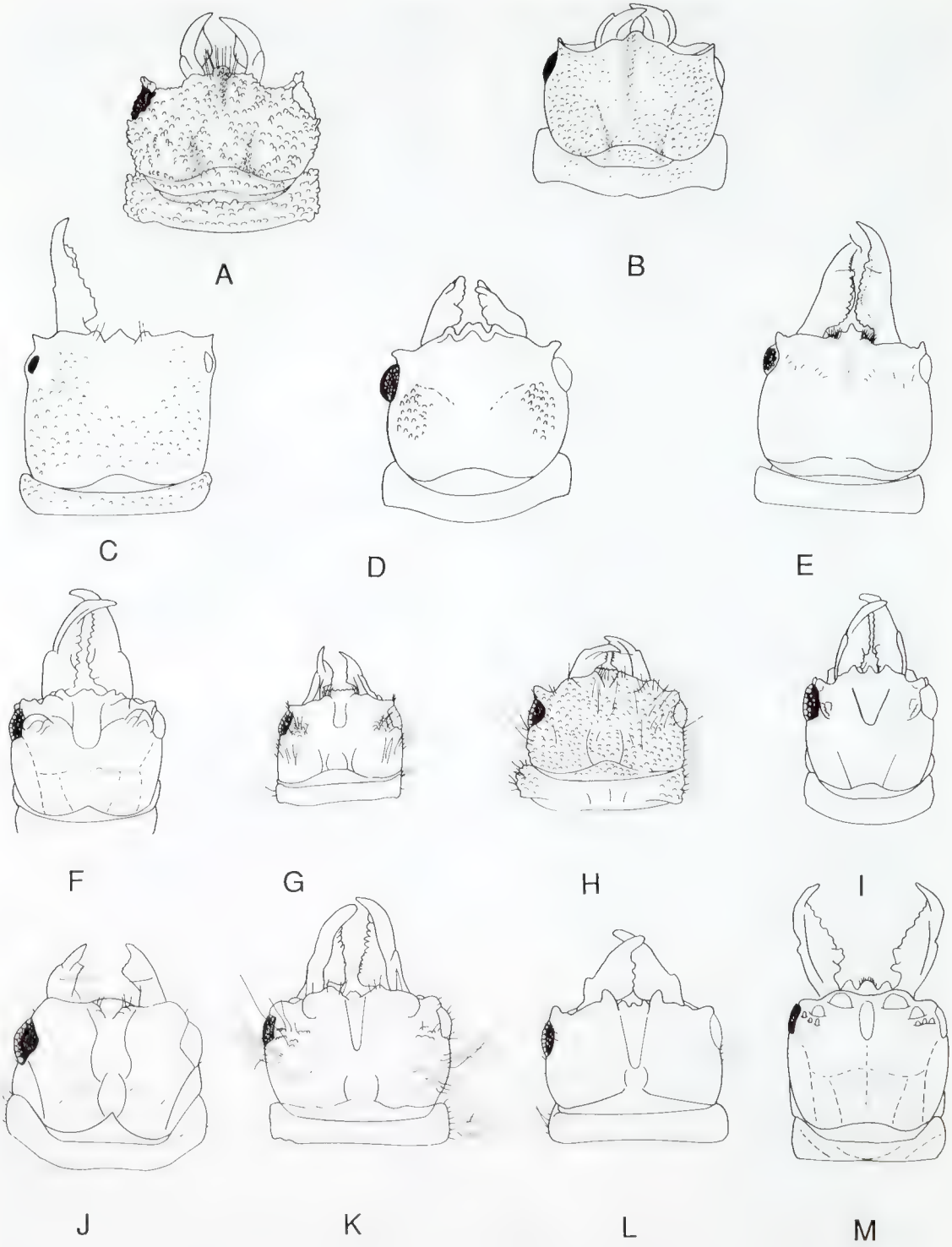
Hennigian phylogenetic (cladistic) methods were used to generate cladograms as hypotheses of the relationship between species of the family Gnathiidae. As many species as were practical, rather than the nominal genera, were chosen for the analysis because of doubt about the monophyly of some genera. The information on character states comes mostly from illustrations and descriptions in the literature and was supplemented from specimens in the collections of the Museum of Victoria. Published details on many species were inadequate for this purpose. These species were omitted but it is felt that the 95 species described in sufficient detail covered the range of form seen in the family. Specimens of *Euneognathia gigas* (Beddard, 1886), *Paragnathia formica* (Hesse, 1864) and *Gnathia maxillaris* (Montagu, 1804) were lent or donated.

The programs PAUP version 3.1.1 and HENNIG86 version 1.5 were used to establish relationships between species and to derive a practical classification which reflected these relationships. The same data set with the same assumptions was run under PAUP with the heuristic search option (general and branch-and-bound) and under HENNIG using *mh** and *bb** routines. Outgroups were chosen from the Isopoda Flabellifera in order to polarise characters. The following sections describe the outgroups, taxa chosen and character transformations.

### *Outgroups*

Brusca and Wilson's (1991) analysis of the relationships of the Isopoda placed the Gnathiidae among the "long-tailed" taxa, part of the non-monophyletic Flabellifera. They concluded that the family no longer deserves the subordinal status traditionally used. Outgroups, therefore, were sought from among the Flabellifera. Wägele and Brandt (1988) suggested that the protognathiid, *Protognathia bathypelagica* (Schultz, 1977) is a "missing link" or intermediate stage between the Cirolanidae and the Gnathiidae, and that these two families are closely related. Brusca and Wilson (1991) argued that *Protognathia* is not closely related to the Gnathiidae but rather Protognathiidae is part of the Cirolanidae-Anuropidae-cymothoid line. They argued that the Cirolanidae is more closely related to the Gnathiidae than Protognathiidae is to Gnathiidae. Both the Cirolanidae and the Protognathiidae were selected as outgroups. *Eurydice acuticauda* Bruce, 1981 was chosen to represent the Cirolanidae for many characters.

*Protognathia bathypelagica* is known only from immature specimens; states describing the sexual characters of adult males are coded as


A
B
C
D
E
F
G
H
I
J
K
L
M

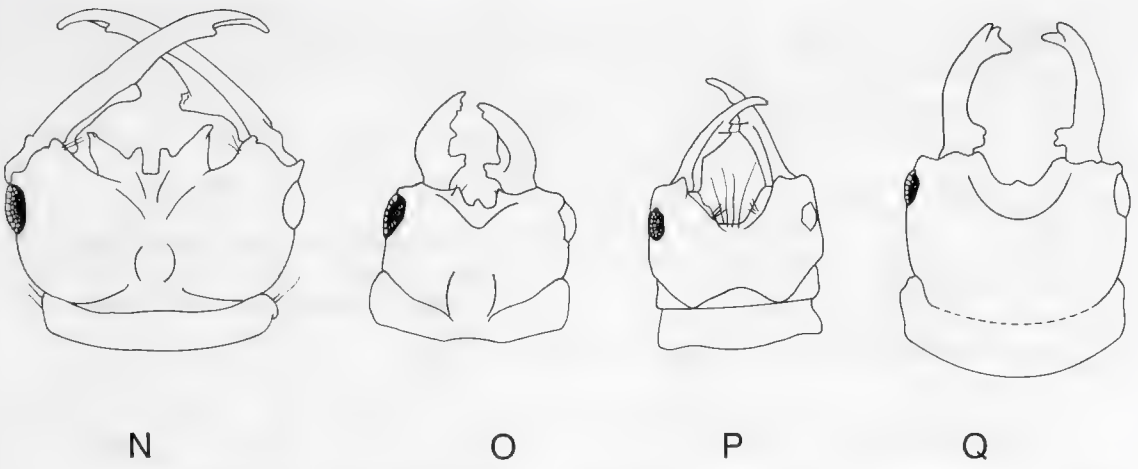



Figure 2. Cephalosomes of 17 Australian species of Gnathiidae not described in this work. A, *Caecognathia agwillisi* (Seed). B, *C. pustulosa* (Hale). C, *Gnathia latidens* (Beddard). D, *G. calamitosa* Monod. E, *G. halei* Cals. F, *G. cornuta* Holdich and Harrison. G, *G. meticola* Holdich and Harrison. H, *G. asperifrons* Holdich and Harrison. I, *G. falcipenis* Holdich and Harrison. J, *G. variobranchia* Holdich. K, *G. biorbis* Holdich and Harrison. L, *G. calmani* Monod M, *G. mulieraria* Hale. N, *Elaphognathia bifurcilla* (Holdich and Harrison). O, *E. forceps* (Holdich and Harrison). P, *E. rimifrons* (Holdich and Harrison). Q, *E. ferox* (Haswell).

Figures copied from original authors except *G. latidens* copied from Monod (1926), and *G. calmani* and *E. ferox* copied from Holdich and Harrison (1980).

unknown (? in Table 3). For both outgroups, a number of the mandibular characters were coded as inapplicable due to the difficulty in drawing homologies between the highly modified mandibles of the Gnathiidae and the mandibles of other Isopoda. Inapplicable characters were coded as states separate from those found in the Gnathiidae (Table 2). The praniza stage of gnathiid ontogeny was also considered when there was difficulty assessing the plesiomorphic condition of some characters.

*Taxa chosen*

It proved impossible to include every described species of Gnathiidae in the analysis. Many species were excluded because they were not described in sufficient detail to enable complete coding of all character states. Ninety-five species from all round the world were included (Table 3) representing all nominal genera and subgenera.

Four species represented the monotypic genera *Euneognathia* (*E. gigas*), *Paragnathia* (*P. formica*), *Heterognathia* (*H. calva*) and *Bythognathia* (*B. yucatanensis*). All species of *Thaumastognathia* were included, three of which are newly described. Of the remaining genera, *Akidognathia*, *Bathygnathia* and *Gnathia*, the type species and all species described in sufficient detail were included in the analysis. Thus, *A. oedipus*, *A. cristatipes*, *B. affinis*, *B. magnifica*, *B. porca* and six similar new species provided data. *Akidognathia* and *Bathygnathia* seemed *a priori* to be closely allied and the 11 species included covered the variation within these two genera and the supposed differences between them, principally in the form of the pereopods, mandibles and frontal border.

The remaining species are or could be members of *Gnathia* and its three subgenera, *Gnathia* s.s., *Perignathia* and *Elaphognathia* as presently defined. The monotypic subgenus *Perignathia* was represented by *P. triospathiona* although its type species is in doubt (see below). *Gnathia* s.s. and *Elaphognathia* were represented by numerous species. *Caecognathia stygia*, type species of a genus considered by Monod (1926) a junior synonym of *Gnathia* was also included.

*Character discussion*

The 72 characters used in the phylogenetic analysis are discussed in turn below. All are potential synapomorphic characters (i.e., none is apomorphic for a single species). The character states are given in Table 2 and the data matrix in Table 3.

*Eyes.* Almost all Gnathiidae have sessile, lateral eyes during all stages of development; this condition is plesiomorphic. Eyes have been lost

Table 2. Character transformations used in the phylogenetic analysis of 95 species of Gnathiidae. The plesiomorphic state is listed first and separated by ; from the apomorphic state or states. In the data matrix plesiomorphic states are indicated by 0 and apomorphic states by 1 or more. Characters with consistency and retention indices of 1 are marked with *.

*Eyes*

1. Eyes present; absent.

*Cephalon*

2. Cephalon broader than long; as long or longer than broad.
3. Dorsal sulcus absent; present.
4. Paraocular ornamentation absent; present.
5. Granules/tubercles absent; present on cephalon; present on cephalon and pereon.
6. Cephalon lacking posterior, laterally deflected grooves; grooves present.
7.* Cephalon lacking anterior median furrow; furrow present.
8. Posterior cephalon not divided by shallow grooves; posterior cephalon divided by grooves (often marked with chromatophores).

*Frontal border*

9. Frontal border rounded/produced; transverse.
10. Frontal border not greatly produced; greatly produced.
11.* Frontal border not excavated; excavated.
12. Frontal border without frontal processes; with frontal processes.
13.* Frontal border not clearly delineated; clearly delineated (chalky white appearance).
14.* Buccal cavity wall not visible dorsally; visible beyond rostrum.
15. Entire frontal margin including region lateral to the base of mandibles not produced; entire margin produced.
16. Frontal border lacking small median indentation; indentation present (not to be confused with excavation found in *Elaphognathia*).
17. Setae on frontal border absent; present.
18. Mediofrontal process absent; single process; multiple processes.
19. Mediofrontal process not inferior; inferior.
20. Superior frontolateral process absent; present.
21. Inferior frontolateral process absent; present.

*Mandible*

22. Armed carina inapplicable; absent; present.
23. Incisura inapplicable; absent; present; pronounced.
24. Internal lobe inapplicable; absent; present.
25. Mandible clearly less than 5 times as long as wide; 5 times as long or longer.
26. Apical cusps absent; present.
27. Blade dentate/crenulate; not dentate; absent/highly reduced.
28. Pseudoblade absent; present.
29. Setae inapplicable; absent; present.

*Antennae*

30. Antenna 1 shorter than or equal to antenna 2; antenna 1 longer than antenna 2.
31. Antenna 1 flagellum with 7 or more articles; 6; 5; 4; 3; 2 or fewer articles.
32. Antenna 2 flagellum with 8 or more articles; 7; 6; 5; 4; 3 or fewer articles.
33.* Antenna 1 peduncle length greater than 4 times width; less than 4 time width.
34.* Antenna relatively straight; curved under mandibles.

*Pereon*

35. Pereon devoid of or with only few setae; setae present anteriorly; setae present all over.
36. Pereon wide (length $\leq$1.85 width); medium; narrow ($\geq$2.5).
37. Pereon pear-shaped (clearly widest at pereonite 5); not pear-shaped.
38. Pereon wider than cephalon; narrower than or as wide as cephalon.
39. Pereonite 1 clearly extending to margins of pereon; surrounded completely by cephalon and pereonite 2; not visible;
40. Anterior constriction of pereonite 4 absent; present.
41. Pereonite 4 lacking mid-dorsal spine; spine present.
42. Pereonite 6 without lobuii; lobuii present.
43. Posterior margin of pereonite 6 not deeply concave; posterior margin deeply concave.

44. Pereonites 5 and 6 not fused; partially fused; completely fused.
45. Pereonite 6 lobuii not conical/globular; lobuii conical/globular [see figs 19, 22, 40].
46. Peronite 7 visible dorsally; not visible.

*Pleon, pleotelson and uropods.*

47. Pleotelson short (as wide or wider than long); medium; long (twice as long or longer than wide).
48. Uropod rami clearly shorter than pleotelson; approximately equal to length; clearly greater than length of pleotelson.
49. Endopod clearly longer than exopod; exopod subequal or longer.

*Maxilliped.*

50. Mouthparts typical of family; small/reduced (difficult to see).
51. Maxilliped of 5 articles; fewer than 5 articles; absent.
52. Palp clearly less than 5 times as long as broad; about 5 times as long as broad.
53. Endite with 4 or more coupling hooks; 1–3 hooks, no hooks.

*Pylopod*

54. Pylopod pediform/cylindrical; slightly widened; operculate (pylopods overlapping)
55. Pylopod of 7 articles; 6; 5; 4; 3 or fewer articles.
56.* Pylopod with no articles greatly enlarged; first article enlarged; second article; first, third and fourth articles enlarged.
57. Article 3 not reduced; reduced; absent.
58. Aerolae absent; present.
59. External margin inapplicable; devoid of plumose setae; a few, well spaced plumose setae; many setae/dense cover.
60. Pylopod inapplicable; with many setae on ventral surface (about 15 or more); few setae; no setae.
61. Article 2 not circular or conical; conical (see figs 21, 24, 36, 42); circular.
62. Spine(s) present on article 3; spines absent.
63.* Ventral surface setae inapplicable; plumose; simple or absent.

*Pereopods*

64. Pereopod setae plumose; simple or absent.
65. Pereopod setae dense; sparse or absent.
66. Pereopod 4 basis lacking distal extension; distal expansion present.
67. Merus of pereopods 3–6 not medially expanded along anteroposterior axis; merus expanded.
68.* Pereopod 4 basis lacking a quadratic lobe; possessing lobe.
69. Pereopod 4 ischium not expanded; ischium expanded; ischium expanded as a cusp.
70. Pereopod 5 ischium not expanded; ischium expanded.

*Pleopods*

71. Pleopods setose; not setose.
72. Appendix masculina inapplicable; greater than or subequal to length of rami; half to three-quarters length of rami; absent.

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in the adults of only a few species, nearly all of which occur in the deep sea (character 1).

*Cephalon.* The dorsal surface of the plesiomorphic cephalon is smooth, featureless and broader than long, similar to the cephalon of the cirolanid, *E. acuticauda*. While the Cirolanidae are mostly free-roaming predators or scavengers (Bruce, 1986), adult Gnathiidae are cryptic, often inhabiting substrate that offers protection. Some species may construct burrows. From within these hiding places the gnathiid's mandibles can protrude to deal with potential trouble while the remainder of the animal remains protected (Seed, 1979). Compared to other Isopoda, the mandibles and cephalon of many gnathiids are strengthened. Apomorphic states of the cephalon include sculpture and ornaments which may increase the strength of the cephalon; these include furrows and depressions and raised bumps and tubercles.

A peculiar feature found mid-dorsally on the anterior cephalon or rostrum of a few gnathiids is a thin translucent region of variable shape and size, located above the buccal cavity. The function of this structure and its evolutionary importance are unknown.

Table 3. Species-character matrix of species of Gnathiidae (95 species by 72 characters). The first two taxa are outgroups. Unknown character states are shown by "?"

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Cirolanidae | 0000000000 | 0000000000 | 0000000000 | 4000000000 | 0000000000 | 0020000010 | 0001100000 | 00 |
| *Protognathia* | 1000000000 | 0000000000 | 0000000000 | 1000011000 | 0000002110 | 0020000000 | 0000000000 | 0? |
| *B. adlerzia* | 0110000001 | 0001002000 | 0132102020 | 2?10021101 | 0100001210 | 0002220012 | 0021000010 | 01 |
| *B. affinis* | 1000000001 | 0001001000 | 0131102011 | 2210021101 | 0000001110 | 0022220032 | 0021101000 | 02 |
| *B. cardicondyla* | 1010200001 | 0001001000 | 0131102020 | 2210021111 | 0110000110 | 0002220012 | 0021000010 | 00 |
| *B. magnifica* | 0110000001 | 0001001000 | 0112102010 | 2010021101 | 011000???0 | 0002220021 | 0?21000021 | 02 |
| *B. oedipus* | 1000000001 | 0001100000 | 0112102010 | 1010021101 | 0100002210 | 0002220021 | 0021000021 | 01 |
| *B. porca* | 1120000001 | 0001001000 | 0131102010 | 2110021101 | 0000001110 | 0002220032 | 0021001010 | 02 |
| *B. tapinoma* | 1000000001 | 0001101000 | 0112102020 | 2010021101 | 0100001210 | 0002220121 | 0021000010 | 01 |
| *B. vollenhovia* | 1000000001 | 0001001000 | 0131102010 | 2210021101 | 0000001210 | 0002220021 | 0021001000 | 02 |
| *Bythognathia* | 1010000001 | 0000000000 | 0131002010 | 0110021101 | 0010000210 | 0000100032 | 0120001000 | 01 |
| *C. abyssorum* | 0000200001 | 0000010000 | 0121001010 | 3210001111 | 0110001210 | 0022411122 | 2121100000 | 12 |
| *C. agwilisi* | 0000211000 | 0000001000 | 0121001010 | 2110110001 | 0002001110 | 0012412012 | 2121000000 | 02 |
| *C. akaroensis* | 0000200000 | 0000011000 | 0221000010 | 3110111111 | 0010000210 | 0022411??? | 2121100000 | 02 |
| *C. branchyponcra* | 0100000000 | 0000001000 | 0111001011 | 2510010010 | 0110101000 | 0122411032 | 1110000000 | 02 |
| *C. calva* | 0000211000 | 0000000000 | 0121001010 | 2110011111 | 0110001110 | 0012411012 | 2121100000 | 12 |
| *C. consobrina* | 0000200000 | 0000011000 | 0121000010 | 2?10011111 | 0110000110 | 0022411132 | 2121100000 | 01 |
| *C. crenulatifrons* | 00?0100001 | 0000000000 | 0111000010 | 2110011101 | 0010001110 | 0022411?32 | 2121100000 | ?2 |
| *C. diacamma* | 0100000000 | 0000001000 | 0111001011 | 2310010000 | 0110100010 | 0122411031 | 1110000000 | 02 |
| *C. dolichoderus* | 0000000001 | 0000001000 | 0231002010 | 22?0211120 | 0110001100 | 0012411012 | 2120000000 | 02 |
| *C. elongata* | 00?0200100 | 0000001000 | 0121001010 | 2110021101 | 0110001110 | 0022411132 | 2121100000 | 12 |
| *C. galzini* | 0000200000 | 0000011000 | 0121001010 | 3210211101 | 0010001210 | 0022412132 | 2121100000 | ?2 |
| *C. gnamptogenys* | 0000000000 | 0000001000 | 0111002010 | 2110211120 | 0110001110 | 0022411131 | 2121010000 | 01 |
| *C. hirsuta* | 0000200001 | 0000001000 | 0121001010 | ?210101110 | 0110001210 | 0022411022 | 2121100000 | 12 |
| *C. huberta* | 0000211000 | 0000001000 | 0221001021 | 3410211111 | 1000000200 | 0012412012 | 2121100000 | 12 |
| *C. leptanilla* | 0100000001 | 0000001000 | 0111001011 | 2310210010 | 0110100110 | 0122411031 | 1111000000 | 02 |
| *C. pactca* | 0000200000 | 0000010000 | 0121000010 | 3110011111 | 0110000210 | 0022411??? | 2121100000 | 02 |
| *C. paratrechia* | 0000211000 | 0000001000 | 022?001020 | 2310210001 | 1000010110 | 0022412011 | 2121100000 | 02 |
| *C. polaris* | 0000211000 | 0000000000 | 0121001010 | 2110011111 | 1010001110 | 0012411032 | 2121100000 | 12 |
| *C. polythrix* | 0000200000 | 0000000000 | 0211001010 | 2110011111 | 0110001210 | 0022411??? | 2121100000 | 02 |
| *C. sanctaecrucis* | 0000200000 | 0000000000 | 0111001010 | 2110211100 | 0100001110 | 0012411131 | 2121000000 | 12 |
| *C. schistifrons* | 000010002? | 0000010000 | 0111001010 | 2110001111 | 0110001210 | 0022411031 | 2121100000 | 12 |
| *C. serrata* | 0000200001 | 0000101000 | 0111002010 | 2110221120 | 0110001110 | 0022411021 | 2121?10000 | 12 |
| *C. trachymesopus* | 0100000000 | 0000001000 | 0111001011 | 2410010010 | 0110101000 | 0122411031 | 1110000000 | 02 |
| *C. wagneri* | 0000000000 | 0000001000 | 0111001011 | 1110021101 | 0100001110 | 0012411132 | 2121100000 | 12 |
| *I. amboinensis* | 0010200010 | 1100000100 | 0112002020 | 3110011120 | 0000000210 | 0022411132 | 2121100000 | 02 |
| *I. bacescoi* | 0010000110 | 1100000201 | 0122101010 | 2110011101 | 0000001210 | 0022412032 | 2121100000 | ?2 |
| *E. bifurcilla* | 0000000010 | 1100001211 | 0112102010 | 2110001111 | 0000000210 | 0022411022 | 2121100000 | 00 |
| *I. ferox* | 0000000010 | 1?00000?00 | 0112112010 | 4110001120 | 0000001210 | 0022411122 | 2121100000 | 02 |
| *I. forceps* | 0010000010 | 1100001100 | 0112001010 | 4010011121 | 0000000210 | 0022412122 | 2121100000 | 02 |
| *I. inovgattella* | 0000000010 | 1100001211 | 1112102010 | 2110001110 | 0000000210 | 0022411022 | 2121000000 | 02 |
| *I. rangifer* | 0000000010 | 1?00000000 | 0112112010 | 3110001120 | 0100000210 | 0022412032 | 2121100000 | 02 |
| *I. sugashimaensis* | 0000000010 | 1100001001 | 0112102020 | 2110011111 | 0000001210 | 0022411032 | 2121100000 | ?2 |
| *E. wolffi* | 0000100010 | 1100001201 | 0112112020 | 3110001120 | 0000000210 | 0022411132 | 2121100000 | ?2 |
| *Luconognathia* | 0011000010 | 0100000200 | 113200011?0 | 2010011110 | 0110002110 | 0011200032 | 0121100000 | 02 |
| *Gibbagnathia* | 0000200000 | 0100001001 | 0111002010 | 3300211111 | 0010000101 | 1020300013 | 0120000000 | 02 |
| *G. albescens* | 1010100011 | 0100101001 | 0121000020 | 2110021011 | 0000001100 | 0012411132 | 2121100000 | ?2 |
| *G. asperifrons* | 0000210010 | 0100001001 | 0121000020 | ?210210000 | 0110001010 | 0022411032 | 2121100000 | 12 |
| *G. beethovem* | 0010000010 | 0100001211 | 0111000020 | 3110211110 | 0000001210 | 0022412032 | 2121100000 | ?2 |
| *G. biorbis* | 0011000010 | 0100001211 | 0121000010 | 2110011101 | 0000001210 | 0022411132 | 2121100000 | 12 |
| *G. calmani* | 0010000010 | 0100001211 | 0121000010 | 2110011101 | 0000000210 | 0022411132 | 2121100000 | 02 |
| *G. camponotus* | 0011200010 | 0100001111 | 0122000110 | 2110011111 | 0000000110 | 0022411132 | 2121100000 | 01 |
| *G. clementensis* | 0010200010 | 0100001211 | 0121000010 | 1110211100 | 0110101110 | 0012411131 | 2121000000 | 02 |
| *G. cooki* | 0011000010 | 0100001211 | 1121000020 | 3210211111 | 0000000210 | 0022411132 | 2121100000 | ?2 |
| *G. connuta* | 0011000110 | 0100001211 | 0122000010 | 2110021101 | 0000001110 | 0022411132 | 2121100000 | 02 |
| *G. coronadensis* | 1010000010 | 0100001111 | 0121000010 | 2110011100 | 0110001200 | 0022411031 | 2121000000 | ?2 |
| *G. epopostruma* | 0011000010 | 0100001200 | 0121000020 | 2110211111 | 0000001210 | 0022411132 | 2121100000 | 02 |
| *G. falcipenis* | 0011010010 | 0100001200 | 0122000010 | 2110021111 | 0000001210 | 0022411132 | 2121100000 | 02 |
| *G. gonzalezi* | 0010000010 | 0100001001 | 0121000020 | 4210211110 | 0010001110 | 0012411022 | 2121100000 | ?2 |
| *G. haleri* | 0010000011 | 0100001111 | 0111000120 | 2110011101 | 0102001100 | 0022411132 | 2121100000 | 01 |
| *G. hlephila* | 0011200010 | 0100000111 | 1121000020 | 2110011111 | 0010001210 | 0022411022 | 2121100000 | 02 |
| *G. inopinata* | 001?200010 | 0100001211 | 0221000010 | 2110011011 | 0000000210 | 0022411??? | 2121100000 | 02 |
| *G. isidomyrmex* | 0010000010 | 0100001211 | 0111000020 | 2110111111 | 0000000210 | 0022411132 | 2121100000 | 01 |
| *G. johanna* | 0010000010 | 0100001111 | 0122000020 | 2110211111 | 0010001210 | 0022412132 | 2121100000 | 12 |
| *G. lanuacapitalis* | 1011000010 | 0100001111 | 0121000010 | 2110021101 | 0100001100 | 0022412032 | 2121100000 | 02 |
| *G. magdalensis* | 0011100010 | 0100001200 | 0122000020 | 2110211121 | 0000001210 | 0022411132 | 2121100000 | ?2 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *G. margaritarum* | 0011200010 | 0100001211 | 1121000020 | 3110211111 | 0000000200 | 0022411132 | 2121100000 | ?2 |
| *G. maxillaris* | 0001200010 | 0100001111 | 0121000010 | 2110011111 | 0000000110 | 0022412132 | 2121100000 | 12 |
| *G. meticola* | 0010000110 | 0100001001 | 0121000010 | 1110011001 | 0000001200 | 0022411032 | 2121100000 | 02 |
| *G. mortensen* | 0020200010 | 0100001101 | 0122000010 | 2110011001 | 0100000210 | 0022411??2 | 2121100000 | 02 |
| *G. mulleraria* | 0010000110 | 0100001111 | 0122000010 | 2110021101 | 0000000110 | 0022411132 | 2121100000 | 02 |
| *G. mystrium* | 0011000010 | 0100001211 | 1121000020 | 2110011121 | 0000001110 | 0022411132 | 2121100000 | 01 |
| *G. necembola* | 0010000010 | 0100001111 | 1121000020 | 3110011101 | 0010001110 | 0022411032 | 2121100000 | ?2 |
| *G. notostigma* | 0011000010 | 0100001200 | 0122000120 | 2110011111 | 0000000110 | 0022411132 | 2121100000 | 01 |
| *G. odontomachus* | 0010000010 | 0100001111 | 0121000020 | 2110211101 | 0000000100 | 0022411132 | 2121100000 | 01 |
| *G. oxyuraea* | 0001000010 | 0100001110 | 0211000020 | 3110011121 | 0010001110 | 0022412132 | 2121100000 | 02 |
| *G. prolasius* | 0011000010 | 0100001200 | 0111000020 | 2110021111 | 0000010210 | 0122411012 | 2121100000 | 12 |
| *G. rathi* | 0010200010 | 0100001001 | 0121000020 | 3110021111 | 0000000200 | 0022411032 | 2121100000 | ?2 |
| *G. regalis* | 0010200010 | 0100000111 | 1121000010 | 3110011111 | 0110000200 | 0022411032 | 2121100000 | 02 |
| *G. thylidoponera* | 0010000011 | 0100001111 | 0111000120 | 2110011111 | 0100001100 | 0022411132 | 2121100000 | 00 |
| *G. samariensis* | 0010000010 | 0100001200 | 0121000010 | 3110201121 | 0000001200 | 0022411132 | 2121100000 | ?2 |
| *G. serrulatifrons* | 0001200010 | 0100001211 | 1121000110 | ??10011111 | 0110001110 | 0022411?32 | 2121100000 | 02 |
| *G. stigmacros* | 0011000010 | 0100001101 | 0111001020 | 2110021111 | 0000010210 | 0112411012 | 2121100000 | 02 |
| *G. triospathiona* | 0000000010 | 0100000100 | 1121001010 | 2010020011 | 0000001110 | 0??2410032 | 11?1100000 | 02 |
| *G. variobranchia* | 0010000010 | 0100001001 | 0121000020 | 2110211011 | 0000000110 | 0022411032 | 2121100000 | 02 |
| *G. vellosa* | 0010200010 | 0100001200 | 0121000010 | 3110201121 | 0000001200 | 0022411132 | 2121100000 | ?2 |
| *G. venusta* | 0011000010 | 0100001111 | 1121000120 | 2110021121 | 0100001?00 | 0022411?32 | 2121000000 | 02 |
| *G. virginalis* | 0010200010 | 0100001200 | 0121000010 | 3110211121 | 0000000210 | 0022412132 | 2121100000 | ?2 |
| *G. vorax* | 0000000010 | 0100001111 | 1121000010 | 2110021111 | 0000001110 | 0022412032 | 2121100000 | 02 |
| *M. colobstruma* | 1010010001 | 0010101000 | 0111001010 | 2110021111 | 0100000110 | 0002220111 | 0021000120 | 02 |
| *M. cristatipes* | 1010000000 | 0020000000 | 0111001010 | 2110021101 | 0110000210 | 0002220012 | 0021000121 | 11 |
| *M. ponera* | 1010000000 | 0010000000 | 0121001010 | 2010021011 | 0100001110 | 0002220011 | 0021000120 | 11 |
| *Paragnathia* | 0010000000 | 0000001000 | 0121000010 | 3010021111 | 0010000210 | 0011130012 | 0120100000 | 12 |
| *L. diceros* | 0000200000 | 0000001000 | 0221000011 | 2501000010 | 0000010111 | 1020300013 | 0121100000 | 11 |
| *L. metaphone* | 0000000010 | 0100001200 | 1111000021 | 4501000010 | 0001010001 | 2020200013 | 0121100000 | 12 |
| *L. orectognathus* | 0000000001 | 0000001000 | 0111000021 | 4401010110 | 0002010201 | 1020300013 | 0121100000 | 12 |
| *L. wasmanna* | 0000000010 | 0000001000 | 0131000021 | 5401200010 | 0001010111 | 2020300013 | 0121100000 | 12 |

Characters 2–8 summarise character changes in the cephalon.

*Frontal border.* The frontal borders of the Gnathiidae are variable and often complex. Monod (1926) introduced terms to describe many of the unique structures found there (see fig. 1). The plesiomorphic frontal border is simple, smoothly rounded, only slightly produced and devoid of setae, similar to that of most cirolanids. The apomorphic frontal border may have one or more frontal processes originating from different vertical levels and may be greatly produced or deeply excavated.

Gnathiids belonging to the Section Transversae (see Monod, 1926) possess a relatively linear frontal border which is punctuated with one or more frontal processes. All species of *Bathygnathia* lack frontal processes but possess a frontal border produced into a rostrum. The rostrum can be as long as the rest of the cephalon beyond which the buccal cavity wall may be visible. The frontal border of *Elaphognathia* has been deeply excavated. The frontal border region of some species of *Monodgnathia* is clearly delineated from the rest of the cephalon and has a chalky-white appearance in the two newly described Australian species.

*Mandibles.* Pronounced, anteriorly protruding mandibles characterise the adult male Gnathiidae. These mandibles are believed to be for display or defence and not involved in feeding (Brusca and Iverson, 1985). Male *Gnathia* have been observed capturing females with its mandibles to gather a harem in its burrow. Homologies between the mandibles of gnathiids and of other isopods are difficult to draw. The molar, spine row and lacinia mobilis are reduced if present. The mandibular palp may be represented by the mandibular seta in gnathiids but this is not assumed.

For the purposes of this analysis, the plesiomorphic state of the mandibles in gnathiids is of a relatively straight and symmetrical mandible with a single dentate blade, homologous to the lacinia mobilis of cirolanids. Monod (1926) introduced new terms to describe what are believed to be features unique to the gnathiid mandible. No homologies are drawn between the internal lobe and molar process of the mandible of other Isopoda and the armed carina and incisura of gnathiids and the incisor process of other isopods. These characters have been coded as inapplicable for the outgroups. Other apomorphic states include the dramatic lengthening

of the mandibles and addition of apical cusps as found in *Elaphognathia*.

Characters 22–29 summarise character changes in the mandibles.

*Antennae.* The antennae are similar to the antennae of other Isopoda: antenna 1 with a 3-articled peduncle and a short first flagella article; antenna 2 with a 5-articled peduncle. The first article of antenna 2 is very short and not figured in gnathiid illustrations. Reduction in the number of antennal flagella articles, reduction in width of the peduncle of antenna 1, and reduction in the length of antenna 2 (relative to antenna 1) are all apomorphic states.

Characters 30–34 refer to the antennae.

*Pereon.* The Gnathiidae differ considerably from the body plan of Cirolanidae. Many gnathiids have a more elongate and flexible habitus; are proportionally narrower and longer, and are better articulated between pereonites 3 and 4 (characters 36–38 and 40).

Cephalisation is characteristic of the Gnathiidae, pereonite 1 is partially fused with the cephalon in all species. Further cephalisation has occurred in a few species; pereonite 1 has become immersed or completely fused with the cephalon (character 39). Pereonite 7 is reduced and appears to form part of the pleon. In a few species, pereonite 7 is not visible dorsally. Various ornamental changes of unknown function have also occurred and are summarised in characters 41–43 and 45. These changes may serve to strengthen the pereon which is relatively soft, especially in the pranizas and females.

Pereonites 5 and 6 of pranizas have been completely fused together into an elastic stomach region (Wägele, 1987). Pranizas are able to engorge themselves on their fish host (Paperna and Por, 1977; Wägele, 1987) and this elastic stomach region expands and contracts with the meal. A few adult gnathiids retain this apomorphy (character 44).

*Pleon, pleotelson and uropods.* The tailfan is longer and more slender than the tailfan of Cirolanidae (Wägele, 1987). This may aid in locomotion, particularly for the praniza which must swim to and from suitable fish hosts. The pleotelson of most gnathiids is triangular with a marked apex (though the truncated pleotelson of *C. agwillisi* (Seed) is a notable exception). The uropodal rami of Cirolanidae are short, shorter than or about as long as the pleotelson. Elongation of the rami relative to the pleotelson and of the exopod relative to the endopod are considered apomorphies.

Characters 47–49 summarise these changes.

*Maxilliped.* The plesiomorphic maxilliped is 5-articled with a palp approximately two to three times as long as broad. The maxilliped is similar in most gnathiids; apomorphic changes include the loss of some or all of the coupling hooks found on the internal margin of the endite and the lengthening of the palp to approximately five times its width.

The exceptions are the genera *Thaumastognathia* and *Gibbagnathia* whose maxillipeds are greatly reduced to only one or two articles or lost altogether (characters 50–53).

*Pylopod.* The pylopod is the highly modified pereopod 1 and defines the Gnathiidae. The pylopod is directed anteriorly and forms the most ventral mouthpart. The function of the pylopod has not been fully investigated but it has been suggested that in most genera it acts as a operculate cover for the other mouthparts and/or as a large surface area across which gas exchange takes place (Seed, 1979). An analogue is seen in the third maxilliped of decapods.

The plesiomorphic state of the pylopod, a simple pereopod, is seen in the "gnathopode" of the larval *Paragnathia formica* (Monod, 1926: fig. 34). In adult males of all genera except *Bythognathia* the pylopod is simplified and lacks the terminal unguis. The apomorphic states involve a reduction in the number of articles from more than five to as few as three or two, a change from a cylindrical shape to an operculate shape and the loss of setae. The fringe of plumose setae seen on the external margin of article 1 on the pylopod of many species has been secondarily derived and is not directly homologous with any setae on a typical pereopod. This condition is apomorphic.

Characters 54–63 are changes in the pylopod.

*Pereopods.* Adult gnathiids have only five pairs of functional walking legs: thoracopods 3–7 or pereopods 2–6 of other isopods. Pereopod 1 has been modified into the pylopod and pereopod 7 is absent, a neotenous state shown in all isopod mancas (first instar). The five remaining pereopods (2–6 in our numbering) primitively are very similar to each other and to the pereopods of other isopods except for a dense covering of plumose setae. Pranizas use these plumose setae to swim towards a suitable fish host (Wägele and Brandt, 1988).

The proportions of the basis, ischium and merus on pereopods 4–6 are diagnostic of species of *Bathygnathia* and *Monodgnathia*. The

merus of pereopods 4–6 in some species of *Bathygnathia* is medially expanded along the anteroposterior axis. The ischium of pereopod 4 of species of both *Monodgnathia* and *Bathygnathia* may be distally expanded, occasionally as a circular cusp which appears to function as a large foot or support. The distal articles below the ischium cusp can be directed along the same plain as the ventral face of the cusp further increasing the surface area available for support; these articles no longer appear to be part of a functional walking leg (see *Monodgnathia ponera*). The ischium of pereopod 5 may also be expanded. The basis of pereopod 4 of some species previously assigned to *Akidognathia* has developed a pronounced quadratic lobe on the lateral face (see figs 74 and 76). The function of this structure has not been investigated though it appears to be capable of locking pereopod 4 against the pereon.

Characters 64–70 explain changes in pereopods.

*Pleopods and penes*. The pleopods are useful taxonomic characters for the study of many crustacean taxa but do not vary greatly among species of Gnathiidae. The plesiomorphic pleopods have setose margins (e.g., Cirolanidae) and the appendix masculina is as long or longer than the endopod of pleopod 2. Loss of setae from the pleopodal rami (character 71) and reduction (character 72, state 1) or loss (state 2) of the appendix masculina are apomorphic states. The penes of most gnathiids are small; only in a few species are they greatly enlarged.

## Results

*Cladogram*

While processing earlier versions of the data matrix using the programs PAUP and HENNIG it was not uncommon for one program to find shorter trees than the other. Neither program consistently found the shorter trees, therefore, when dealing with large data sets we strongly recommend that more than one tree-calculating program is used.

For the final data matrix (Table 2) both HENNIG, using the *mh** and *bb** search options, and PAUP, using the heuristic search option, found equally parsimonious trees of the same length – 594 steps (consistency index = 0.19, retention index = 0.63).

Almost 1000 equally parsimonious trees were saved by HENNIG and 3000 trees by PAUP but given the limited memory available on the computers used for the analysis, the number of trees saved represent only a fraction of the true number of equally parsimonious trees for this data set. Because of the large number of equally parsimonious trees found it was necessary to calculate consensus trees with their resulting loss of information and resolution. Nelson strict-consensus and 50% majority-rule trees were generated. These differed from each other only at the subgeneric level, the major clades which could be used to define genera were identical in both. Numerous versions and subsets of the data matrix supported the major clades, therefore, we are confident of the monophyly of these major clades. The strict consensus tree is shown in fig. 3. Two major clades are evident. The smaller clade is comprised solely of the genus *Thaumastognathia*; the other clade contains the remaining nine genera.

Ten characters (14%) retained ci and ri equal to 1 and are marked with * in Table 2. A further 15 characters (21%) had ci equal to or greater than 0.5.

The transformation series, apomorphic changes at all nodes of the cladogram, were investigated using the *apolist* option in PAUP and the program CLADOS. Ambivalent characters were revealed with the *xs h* option in HENNIG86. Thirty-two characters were ambivalent at one or more nodes; 18 occurred at nodes that separated the major clades. The implication of this is that these characters could not be used in defining genera unless post hoc decisions on their value were made.

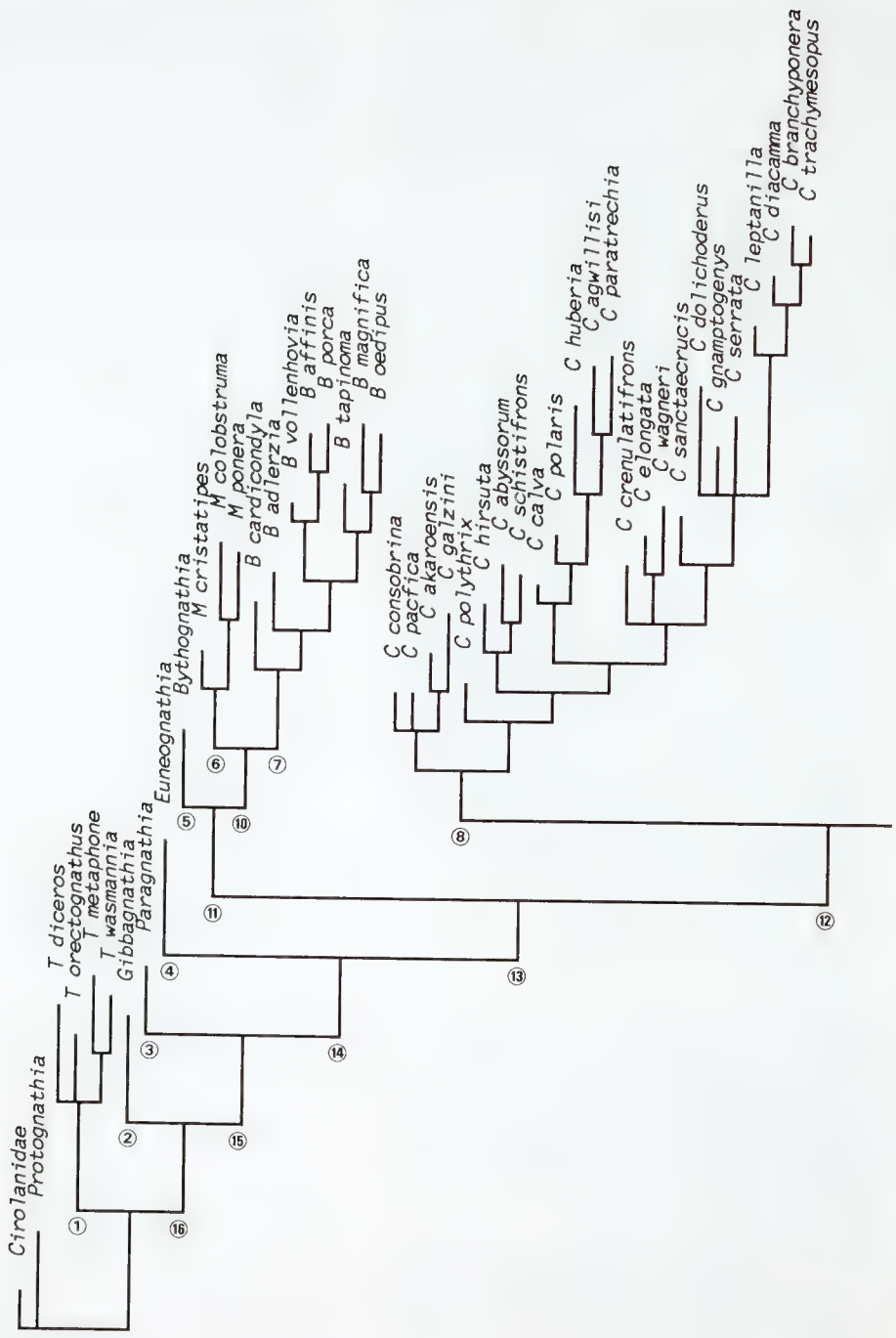
The successive weighting option (PAUP *reweight*) resulted in longer equally parsimonious trees (after weights had been reconverted to unity). These trees resolved some clades, principally within the *Caecognathia* and *Gnathia* clades, suggesting that a more robust analysis may reveal that these two genera can be further divided and refined. Because of their greater length, trees generated by the successive weight option were not considered further.

*Character changes defining clades and genera*

Character changes defining the major clades are discussed below. The major clades for which taxonomic status exists or is proposed are outlined and discussed in further detail. No conclusion is drawn about the relationship of the Gnathiidae to the outgroups.

The family is divided into two clades, 1 and 16, interpreted as one and nine genera respectively.

*Thaumastoganthia* (clade 1) shares the following apomorphies that are never reversed:


Cirolanidae
Protognathia
T diceros
T orectognathus
T metaphone
T wasmannia
Gibbagnathia
Paragnathia
Euneognathia
Bythognathia
M cristatipes
M colobstruma
M ponera
B cardicondyla
B adlerzia
B vollenhovia
B affinis
B porca
B tapinoma
B magnifica
B oedipus
C consobrina
C pacifica
C akaroensis
C galzini
C polythrix
C hirsuta
C abyssorum
C schistifrons
C calva
C polaris
C huberia
C agwillisi
C paratrechia
C crenulatifrons
C elongata
C wagneri
C sanctaecrucis
C dolichoderus
C gnamptogenys
C serrata
C leptanilla
C diacamma
C branchyponera
C trachymesopus
①
②
③
④
⑤
⑥
⑦
⑧
⑩
⑪
⑫
⑬
⑭
⑮
⑯

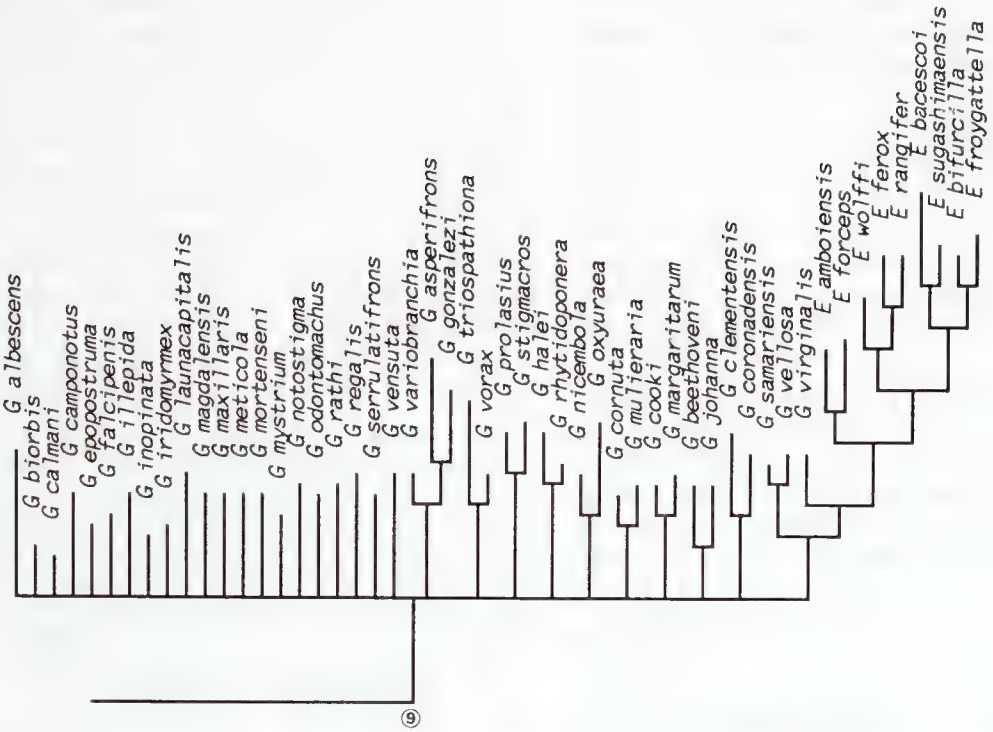



Figure 3. Strict consenus tree calculated from over 3000 equally parsimonious trees (The tree does not indicate branch length but is organised for clarity only).

mouthparts small; maxilliped of fewer than 5 articles; antenna curved under mandibles; antenna 1 longer than antenna 2, antenna 2 peduncle stout (less than 4 times width) and flagellum of 3 articles or less; pereonite 7 not visible dorsally and pleopods without setae. The following plesiomorphies also unite *Thaumastognathia*: pylopod pediform, not operculate and pereon widest at pereonite 5.

Clade 16 (*Gibbagnathia*, *Paragnathia*, *Euneognathia*, *Bythognathia*, *Monodgnathia*, *Bathygnathia*, *Caecognathia*, *Gnathia* and *Elaphognathia*) share the following characters that are sometimes reversed: antenna 1 flagellum of four or more articles; pereon even-sided; pereonite 4 possessing an anterior constriction; pereonite 7 visible and antenna 2 longer than or subequal to antenna 1.

*Gibbagnathia* (clade 2) is a monotypic genus defined by numerous autapomorphies not included in this analysis (see *Methods*). In this analysis *Gibbagnathia* is characterised by the following apomophies convergent in other taxa: mouthparts small; pylopod pediform; maxilliped of fewer than 5 articles; frontal border with processes; superior frontolateral process present; mandibular blade reduced or absent and cephalon and pereon covered with numerous granules and setae.

Clade 15 unites eight genera which share the following characters that are sometimes reversed: mouthparts not reduced; pylopod not pediform, with setae on ventral surface; maxilliped of 5 articles (sometimes with coupling hooks); antenna 1 peduncle length greater than four times width and dorsal sulcus present.

*Paragnathia* (clade 3) is also a monotypic genus defined by numerous autapomorphies not included in this analysis (see Monod, 1926). In this analysis *Paragnathia* is characterised by the following which are convergent in other taxa: pylopod 6-articled, operculate (articles 1, 3 and 4 enlarged); frontal border without processes; pleopods without setae; pereopods covered in plumose setae and uropodal rami clearly extending beyond the apex of the pleotelson.

Clade 14 unites seven genera with the following synapomorphies that are sometimes reversed: pylopod of 5 or fewer articles (except *Bythognathia*) and external margin of pylopod with at least a few setae.

*Euneognathia* (clade 4) is a monotypic genus defined in this analysis by the following apomophies convergent in other taxa: pylopod 5-articled (not operculate), with a dense margin of plumose setae; frontal border transverse, with processes; mediofrontal process with multiple projections; inferior lateral process present; mandibles with a pseudoblade and an internal lobe; cephalon with paraocular ornamentation; and posterior border of pereonite 6 deeply concave with lobuii. For a complete description, including autapomorphies not used in this analysis see Monod (1926).

Clade 13 unites the seven remaining genera which possess an operculate pylopod (except *Bythognathia*).

Clade 11 links three genera *Bythognathia*, *Monodgnathia* and *Bathygnathia* who share three apomophies, never reversed: produced frontal border; absence of a dentate mandibular blade and presence of four or more coupling hooks on the maxillipedal endite. Other character changes are reversed in some species or genera. These include: absence of eyes (present in two species of *Bathygnathia*) and appendix masculina one-half to three-quarters length of the pleopodal endopod. *Bythognathia* (clade 5), the least derived genus, is monotypic and defined by numerous autapomorphies (Camp, 1988 for complete description). *Bythognathia* is defined in this analysis by the following apomorphies convergent in other taxa: antenna 1 flagellum 7-articled; uropodal rami clearly extending beyond the apex of pleotelson; pylopod 6-articled, pediform, external margin with dense cover of plumose setae; pereonite 1 extending to lateral margins of pereon; pereopods with dense cover of plumose setae and pereopods 3–6 with laterally expanded merus.

*Monodgnathia* and *Bathygnathia* form a strong and consistent group (clade 10) based primarily on the structure of the pylopod. These two genera share synapomorphies: pylopod 5-articled, operculate; pylopod article 2 greatly enlarged with spine(s) present on article 3. *Monodgnathia* (clade 6) is further defined by synapomorphies: mandibular blade present; pereopod 4 basis with a lateral quadratic lobe, ischium distally expanded into a circular cusp and frontal border as a distinct (chalky white in Australian species) region. *Bathygnathia* (clade 7) is defined by one synapomorphy and two apomorphies convergent in other taxa: buccal cavity wall protruding beyond rostrum, frontal border greatly produced and the presence of setae on the frontal border. Other apomorphies reversed in some species include: mandibles long (length about 5 times width); pereopods 3–6 with laterally expanded merus and the ischium of pereopod 4 expanded distally (though not necessarily as a circular cusp).

Clade 12, comprising *Caecognathia* and *Gnathia*, is defined by three apomorphies, all of which involve the pylopod: pylopod 2- or 3-articled, article 1 enlarged and article 3 reduced. Other apomorphic character changes that are reversed in some species include: pylopod with dense margin of plumose setae and article 2 of pylopod circular. *Caecognathia* (clade 8) is defined by three apomorphies reversed in some species: a rounded frontal border; a mandibular blade which is not dentate or crenulate (reversed in *P. crenulatifrons*) and pleopods without setae.

Clade 9 is characterised by two non-reversed apomorphies of the frontal border: frontal border transverse and with processes. Two other apomorphies are reversed in some species: the presence of a superior frontolateral process and a mandibular incisor. This clade contains 56 species previously allocated to *Gnathia* and *Elaphognathia*.

Our analysis did not result in further dichotomies between major clades. The species *G. triospathiona* Boone, which Monod (1926) placed in the subgenus he incorrectly called *Perignathia*, was not significantly different from other species of *Gnathia*. Nine species belonging to the subgenus *Elaphognathia* did cluster in a monophyletic clade sharing several synapomorphies: frontal border excavated, mandibles possessing an internal lobe and lacking a dentate blade. Other character changes are reversed in some species: mediofrontal process and mandibular seta absent. Recognition of this taxon relies on recognition of a paraphyletic nominal taxon *Gnathia*. *Elaphognathia*, with its deeply

excavated frontal border, is immediately distinguishable from *Gnathia*, therefore, both *Elaphognathia* and *Gnathia* are given generic status.

*A new classification of Gnathiidae*

Monod (1926) in his major revision of the Gnathiidae recognised six genera: *Akidognathia, Thaumastognathia, Paragnathia, Euneognathia, Bathygnathia* and *Gnathia*. The genus *Gnathia* was further divided into three subgenera; *Gnathia, Elaphognathia* and "*Perignathia*". Since then, *Bythognathia* was erected by Camp (1988). Of these genera and subgenera *Euneognathia, Bythognathia, Paragnathia* and *Thaumastognathia* remain as originally defined but a new classification is needed for the others.

The strict-consensus tree, the most conservative consensus tree, gives a good deal of confidence in the robustness of the clades and is used as an hypothesis on which to base a new classification as follows:

Family Gnathiidae Leach, 1814
- *Bathygnathia* Dollfus, 1901
- *Bythognathia* Camp, 1988
- *Caecognathia* Dollfus, 1901
- *Elaphognathia* Monod, 1926
- *Euneognathia* Stebbing, 1893
- *Gibbagnathia* gen. nov
- *Gnathia* Leach, 1814
- *Monodgnathia* gen. nov.
- *Paragnathia* Omer-Cooper and Omer-Cooper, 1916
- *Thaumastognathia* Monod, 1926

The significant taxonomic changes proposed by this classification are:

1. Synonymy of the genus *Akidognathia* Stebbing, 1913 with *Bathygnathia* as a result of its type species being placed in the clade containing all species of *Bathygnathia*.
2. Erection of a new genus *Monodgnathia* to house non-type members of the former genus *Akidognathia*.
3. Erection of a new genus (presently monotypic) *Gibbagnathia*.
4. Resurrection of the genus *Caecognathia* based largely on the Section Productae of *Gnathia* (Monod, 1926).
5. Restriction and redefinition of the genus *Gnathia* as a paraphyletic taxon.
6. Elevation of the subgenus *Elaphognathia* to generic status on the basis of monophyly.
7. Synonymy of the subgenus *Perignathia* Monod, 1926 with *Caecognathia*.
8. Synonymy of the genus *Heterognathia* Amar and Roman, 1974 with *Caecognathia* (see Wägele, 1987).

Table 4 lists all currently known species in the new classification.

## Biogeography

The family Gnathiidae is widespread, found from the Arctic through to the Antarctic and the intertidal, shelf and upper slopes of the major oceans. The South Atlantic, Indian Ocean and the Eastern Pacific Ocean have yielded few species of Gnathiidae compared to the seas around Europe, the Caribbean and the Western Pacific. Whether this reflects the amount of taxonomic work undertaken in the various regions or a natural pattern is unclear, though there is no *a priori* reason to expect the Pacific and Indian Oceans to possess a less diverse gnathiid fauna.

The cladogram contains information about the evolution of the family. The most significant evolutionary events in the radiation of the Gnathiidae took place in the cold and cool waters of the southern hemisphere. *Thaumastognathia*, four species on the shelf of Australia-New Zealand, is the sister group of all other gnathiids. Its presence on coasts on both sides of the Tasman Sea indicates that the genus is at least 80 million years old, the time usually given for the separation of these two land masses. The monotypic *Gibbagnathia*, the second clade in the cladogram is also a southern Australian shelf species. *Paragnathia* is enigmatic in being a single Afro-European species but *Euneognathia* is a single species from the Antarctic shelf.

None of these four genera has radiated successfully. But the next clade of three genera has begun to radiate in cold water. *Bythognathia* (one species) is from the deep sea (4000 m) of the Caribbean. *Monodgnathia* (four species) and *Bathognathia* (12 species) are both confined to the slope and deep sea (245–2698 m). *Monodgnathia* has a very disjointed distribution between the Western Pacific and North Atlantic suggesting that further species await discovery. But radiation has been moderate and with the exception of the one species of *Bythognathia* none is found very deep, unlike many other families of isopods.

Two related clades have radiated strongly in more shallow and warmer waters: *Caecognathia* with 43 species distributed more towards the poles than *Gnathia-Elaphognathia* (89 species) which is more cosmopolitan on temperate and tropical shelves and upper slopes. *Elaphogna-*

Table 4. Species of Gnathiidae assigned to genera according to the new classification proposed here. See Monod (1926) for full synonymies of species published by him or prior to this date. Later authorities are included in the References.

*Bathygnathia* Dollfus, 1901
*B. adlerzia* sp. nov.
*B. affinis* Birstein, 1963
*B. bathybia* (Beddard, 1886)
*B. cardiocondyla* sp. nov.
*B. curvirostris* Richardson, 1909
*B. magnifica* Moreira, 1977
*B. monodi* Cals, 1974
*B. oedipus* (Stebbing, 1913)
*B. porca* Kensley, 1980
*B. segonzaci* (Cals, 1982)
*B. tapinoma* sp. nov.
*B. vollenhovia* sp. nov.

*Bythognathia* Camp, 1988
*B. yucatanensis* Camp, 1988

*Caecognathia* Dollfus, 1901
*C. abyssorum* (Sars, 1872)
*C. agwillisi* (Seed, 1979)
*C. akaroensis* (Monod, 1926)
*C. albescenoides* (Menzies, 1962a)
*C. amakusaensis* (Nunomura, 1992)
*C. antarctica* (Studer, 1883)
*C. bicolor* (Hansen, 1916)
*C. branchyponera* sp. nov.
*C. caeca* (Richardson, 1911)
*C. calva* (Vanhöffen, 1914)
*C. consobrina* (Monod, 1926)
*C. coralliophila* (Monod, 1926)
*C. crenulatifrons* (Monod, 1926)
*C. diacamma* sp. nov.
*C. dolichoderus* sp. nov.
*C. elongata* (Kröyer, 1847)
*C. floridensis* (Menzies and Kruczynski, 1983)
*C. galzini* Müller, 1989c
*C. gnamptogenys* sp. nov.
*C. hirsuta* (Sars, 1877)
*C. hodgsoni* (Vanhöffen, 1914)
*C. huberia* sp. nov.
*C. kikuchii* (Nunomura, 1992)
*C. leptanilla* sp. nov.
*C. nasuta* (Nunomura, 1992)
*C. nipponensis* (Monod, 1926)
*C. pacifica* (Monod, 1926)
*C. paratrechia* sp. nov.
*C. pilosipes* (Monod, 1926)
*C. polaris* (Hodgson, 1902)
*C. polythrix* (Monod, 1926)
*C. pustulosa* (Hale, 1924)
*C. regalis* (Monod, 1926)
*C. robusta* (Sars, 1879)
*C. saikaiensis* (Nunomura, 1992)
*C. sanctaecrucis* (Schultz, 1966)
*C. schistifrons* (Stebbing, 1913)
*C. serrata* (Richardson, 1909)
*C. stygia* (Sars, 1877)
*C. trachymesopus* sp. nov.
*C. vanhoeffeni* (Menzies, 1962c)
*C. vemae* (Menzies, 1962a)
*C. wagneri* (Monod, 1925a)

*Elaphognathia* Monod, 1926
*E. amboinensis* (Cals, 1978)
*E. bacescoi* (Bacescu, 1960)
*E. bifurcilla* (Holdich and Harrison, 1980)
*E. cornigera* (Nunomura, 1992)
*E. discolor* (Nunomura, 1988)
*E. ferox* (Haswell, 1884)
*E. forceps* (Holdich and Harrison, 1980)
*E. froygattella* sp. nov.
*E. insolita* (Stebbing, 1905)
*E. lucanoides* (Monod, 1926)
*E. monodi* (Gurjanova, 1936)
*E. rangifer* (Monod, 1926)
*E. rimifrons* (Holdich and Harrison, 1980)
*E. sugashimaensis* (Nunomura, 1981)
*E. wolffi* (Müller, 1989a)

*Euneognathia* Stebbing, 1893
*E. gigas* (Beddard, 1886)

*Gibbagnathia* gen. nov.
*G. europalothrix* sp. nov.

*Gnathia* Leach, 1814
*G. africana* Barnard, 1914
*G. albescens* Hansen, 1916
*G. alces* Monod, 1926
*G. asperifrons* Holdich and Harrison, 1980
*G. beethoveni* Paul and Menzies, 1971
*G. biorbis* Holdich and Harrison, 1980
*G. bungoensis* Nunomura, 1982
*G. calamitosa* Monod, 1926
*G. calmani* Monod, 1926
*G. calsi* Müller, 1993b
*G. camponotus* sp. nov.
*G. clementensis* Schultz, 1966
*G. cooki* Müller, 1989c
*G. cornuta* Holdich and Harrison, 1980
*G. coronadensis* Schultz, 1966
*G. crytopais* Barnard, 1925
*G. dentata* (Sars, 1872)
*G. derzhavini* Gurjanova, 1933
*G. disjuncta* Barnard, 1920
*G. epopstruma* sp. nov.

*G. falcipenis* Holdich and Harrison, 1980
*G. fallax* Monod, 1926
*G. firingae* Müller, 1991
*G. gonalezi* Müller, 1988
*G. halei* Cals, 1973
*G. hirayamai* Nunomura, 1992
*G. illepida* Monod, 1923
*G. incana* Menzies and George, 1972
*G. inopinata* Monod, 1925b
*G. iridomyrmex* sp. nov.
*G. johanna* Monod, 1926
*G. lacunacapitalis* Menzies and George, 1972
*G. latidens* (Beddard, 1886)
*G. lignophila* Müller, 1993a
*G. magdalenensis* Müller, 1988
*G. malaysiensis* Müller, 1993a
*G. margaritarum* Monod, 1926
*G. maxillaris* (Montagu, 1804)
*G. meticola* Holdich and Harrison, 1980
*G. mortenseni* Monod, 1926
*G. mulieraria* Hale, 1924
*G. mystrium* sp. nov.
*G. nicembola* Müller, 1989b
*G. notostigma* sp. nov.
*G. odontomachus* sp. nov.
*G. oxyuraea* (Lilljeborg, 1855)
*G. panousei* Daguerre de Hureaux, 1971
*G. phallonajopsis* Monod, 1925b
*G. philogona* Monod, 1926
*G. piscivora* Paperna and Por, 1977
*G. productatridens* Menzies and Barnard, 1959
*G. prolasius* sp. nov.
*G. puertoricensis* Menzies and Glynn, 1968
*G. rathi* Kensley, 1984
*G. rectifrons* Gurjanova, 1933
*G. rhytidoponera* sp. nov.
*G. samariensis* Müller, 1988
*G. schmidti* Gurjanova, 1933
*G. serrulatifrons* Monod, 1926
*G. steveni* Menzies, 1962b
*G. stigmacros* sp. nov.
*G. taprobansis* Monod, 1926
*G. teisseri* Cals, 1972
*G. tridens* Menzies and Barnard, 1959
*G. trilobata* Schultz, 1966
*G. triospathiona* Boone, 1918
*G. tuberculata* Richardson, 1910
*G. tuberculosa* (Beddard, 1886)
*G. variobranchia* Holdich and Harrison, 1980
*G. vellosa* Müller, 1988
*G. venusta* Monod, 1925b
*G. virginalis* Monod, 1926
*G. vorax* (Lucas, 1849)

*Monodgnathia* gen. nov.
*M. colobostruma* sp. nov.
*M. cristatipes* (Stebbing, 1913)
*M. ponera* sp. nov.
*M. poteriophora* (Monod, 1926)

*Paragnathia*
Omer-Cooper and Omer-Cooper, 1916
*Paragnathia formica* (Hesse, 1864)

*Thaumastognathia* Monod, 1926
*T. diceros* Monod, 1926
*T. metaphone* sp. nov.
*T. orectognathus* sp. nov.
*T. wasmannia* sp. nov.

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*thia* is confined to the Indo-West Pacific region except for one species, *E. bacescoi*, which is from the Mediterranean. Most species of *Elaphognathia* are confined to warm waters.

Holdich and Harrison (1980) suggested that more Australian species of Gnathiidae would be discovered once detailed surveys were completed in regions which had yet to be investigated. Sampling of the Australian coast, shelf and slope has yielded 28 new species of Gnathiidae, more than doubling the number of described Australian species to 45, of these 34 are found in the south-east. To date, only a few areas of northern Australia and no areas in the south-west have been intensively surveyed. Even in regions where detailed work has been carried out not all the potential habitats have been fully investigated. Further sampling is bound to yield more species of Gnathiidae.

Though only limited areas of the Australian coastline have been sampled, it is still clear that the continent possesses an extremely rich and diverse gnathiid fauna in intertidal, shelf and slope environments (Table 5). About one quarter of all the presently described species of Gnathiidae are found in Australian waters. All but three monotypic genera (*Bythognathia*, *Euneognathia* and *Paragnathia*) are represented.

Cals (1973) and Holdich and Harrison (1980) argued that it was premature to state that Australia has an endemic fauna but it now seems certain that this is true for at least southern Australia. The northern boundary along the eastern coast and the western boundary of all species are uncertain because of absence of sampling but there is little overlap between this fauna and the fauna of tropical Australia recorded by Holdich and Harrison. *G. calmani*, described from Vic-

Table 5. Habitat and distributional data for Australian Gnathiidae following format of Holdich and Harrison (1980: table 1) and incorporating new species and range extensions for previously described species from collections of the Museum of Victoria.

| Species | Substratum | Depth (m) | Locality |
|---|---|---|---|
| *Bathygnathia alderzia* sp. nov. | | 780–795 | NW Coral Sea |
| *B. cardiocondyla* sp. nov. | silt to clay | 868–1730 | Off Freycinet Peninsula, Tas. and off Terrigal, NSW |
| *B. opisthopsis* sp. nov. | | 2632–2698 | E of Newcastle, NSW |
| *B. vollenhovia* sp. nov. | coarse shelly sand | 800 | 47 km S of Cape Conran, Vic. and W coast of South Island, New Zealand |
| *Caecognathia agwillisi* (Seed, 1979) | tubes of *Rhampobrachium* sp. and colonies of *Galeolaria* sp. | intertidal | Aireys Inlet, Vic. and Elliston, SA |
| *C. branchyponera* sp. nov. | muddy coarse shell with many sponges | 400–426 | Nowra, NSW to Point Hicks, Vic. |
| *C. diacamma* sp. nov. | fine to coarse sand | 15–103 | Western Bass Strait and S of Newcastle, NSW |
| *C. dolichoderus* sp. nov. | fine to muddy sand | 110–130 | Eastern Bass Strait and E of Cape Banks, NSW |
| *C. gnamptogenys* sp. nov. | | 1000 | S of Point Hicks, Vic. |
| *C. huberia* sp. nov. | mud, sand and hard bottom and sponges | 27–185 | Bass Strait and Broken Bay, NSW |
| *C. leptanilla* sp. nov. | sand and shell | 22–800 | Bass Strait, E coast of Tas. and E of Sydney, NSW |
| *C. paratrechia* sp. nov. | shaded, sessile invertebrates | 20 | Pearson I., SA |
| *C. pustulosa* (Hale, 1924) | sponge | intertidal | Glenelg, SA |
| *C. trachymesopus* sp. nov. | mud to coarse sand with shells | 21–293 | Bass Strait |
| *Elaphognathia bifurcilla* (Holdich and Harrison, 1980) | sand | 10–18.2 | Bowling Green Bay, Qld |
| *E. ferox* (Haswell, 1884) | sand, silt clay and sessile invertebrates / plant holdfasts | intertidal–24 | Port Jackson, NSW to Portland, Vic. |
| *E. forceps* (Holdich and Harrison, 1980) | coral rubble on muddy shore | intertidal | Rowes Bay, Qld |
| *E. froggattella* sp. nov. | coarse sand | 84 | 35 km SSW of Cape Otway, Vic. |
| *E. rimifrons* (Holdich and Harrison, 1980) | sandy mud | 6.8–8.8 | Halifax Bay, Qld |
| *Gibbagnathia europalothorix* sp. nov. | medium to coarse sand | 36–104 | Bass Strait |
| *Gnathia asperifrons* Holdich and Harrison, 1980 | rock scrapings | intertidal | Lizard I., Qld |
| *G. biorbis* Holdich and Harrison, 1980 | dead coral / barnacles | intertidal | Heron I. and Townsville, Qld |
| *G. calamitosa* Monod, 1926 | coarse sand to mud | 29–204 | Nowra, NSW to Eddystone Point, Tas. and west into central Bass Strait |
| *G. calmani* Monod, 1926 | sand, bryozoans and dead coral | intertidal–113 | Heron I., Qld and Portland, Vic. |
| *G. camponotus* sp. nov. | muddy to coarse sand and shell | 55–135 | Bass Strait and E of Port Jackson, NSW |
| *G. cornuta* Holdich and Harrison, 1980 | *Teredo*-bored wood | intertidal | Pallarenda, Qld |
| *G. epopostruma* sp. nov. | medium sand | 81 | 44 km SW off Cape Otway, Vic. |
| *G. falcipenis* Holdich and Harrison, 1980 | wood/coral | intertidal–80 | Magnetic I. and Lizard I., Qld and North West Shelf, WA |
| *G. halei* Cals, 1973 | fine gravel to mud | 136–188 | Off Moreton I. and Capricorn Channel, Qld |
| *G. iridomyrmex* sp. nov. | red coralline algal turf | 11 | Portland, Vic. |
| *G. latidens* (Beddard, 1886) | | 12.8 | Flinders Passage, Qld |
| *G. meticola* Holdich and Harrison, 1980 | wood / barnacles | intertidal | Townsville, Qld |
| *G. mulieraria* Hale, 1924 | among *Zostera* sp. | 12.8–14.6 | Vic. to WA |
| *G. mystrium* sp. nov. | muddy sand to shelly sand | 57–130 | Bass Strait |
| *G. notostigma* sp. nov. | coarse sand and gravel | 75–200 | S of Point Hicks, Vic. and off Broken Bay, NSW |
| *G. odontomachus* sp. nov. | find sand and mud to sandy gravel | 8–13 | Western Port, Vic. |
| *G. prolasius* sp. nov. | coarse shelly sand | 363–1000 | Nowra, NSW to Freycinet Peninsula, Tas. |

| | | | |
|---|---|---|---|
| *G. rhytidoponera* sp. nov. | | 296–303 | Western Coral Sea |
| *G. stigmacros* sp. nov. | medium sand to gravel | 27–293 | Eastern Bass Strait |
| *G. variobranchia* Holdich and Harrison, 1980 | coral | intertidal | Heron I., Qld |
| *Monodgnathia colobstruma* sp. nov. | | 1000 | S of Point Hicks, Vic. |
| *M. ponera* sp. nov. | | 1550 | Lord Howe Rise, Tasman Sea |
| *Thaumastognathia metaphone* sp. nov. | shaded, sessile invertebrates | 20 | Pearson I., SA |
| *T. orectognathus* sp. nov. | medium to very coarse sand | 27–200 | Bass Strait |
| *T. wasmannia* sp. nov. | | 122 | 20 km E of Falmouth, Tas. |

toria is also recorded from Heron I., Queensland but this is exceptional. This discovery of extreme endemism on the southern coast is consistent with the generalisations made by Wilson and Allen (1987). The extent to which the tropical Australian species extend into the Indo-West Pacific is unknown because of the low level of sampling elsewhere.

Moreover, even within the small area studied, many species have limited distributional range. The isopod collections of the Museum of Victoria are based on over 400 well-sorted samples of benthos from Bass Strait and the south-eastern Australian slope and of samples from subtidal rocky habitats. Only two species of more than 30 could be said to be moderately well distributed: *Caecognathia leptanilla* with records from 40 samples collected between 22 and 800 metres in Bass Strait and the eastern shelf and slope; and *Caecognathia trachymesopus* from 29 sites in Bass Strait between 21 and 293 metres. All other species are recorded from fewer than 11 samples. The shallow-water species with the greatest geographical range is *G. mulieraria* recorded from Victoria to Western Australia. Because so little collecting has been done in Western Australia the likelihood remains that other species have this sort of distribution.

The south-eastern Australian gnathiid fauna shows evidence of local radiation into endemic species complexes (see cladogram). The *Caecognathia agwillisi*-complex comprises *C. pustulosa* (not included on this analysis but clearly related to this complex), *C. agwillisi*, and *C. paratrechia* in South Australia and western Victoria and *C. huberia* in Bass Strait and New South Wales. The cladogram suggests that the sister taxa of this group are species from Antarctic seas, *C. calva* and *C. polaris*. The *C. trachymesopus*-complex comprises *C. trachymesopus*, *C. leptanilla* and *C. diacamma* from shelf habitats in Bass Strait and south-eastern Australia and *C. branchyponera* from the slope in the same region.

Further evidence of local radiation is seen in *Thaumastognathia* whose four species are confined to the Australian or New Zealand shelf.

Although deep-water Australian species of the genera *Bathygnathia* and *Monodgnathia* are endemic they do not group into local complexes. The species seem to have arisen independently within widespread genera.

The species from the south-eastern slope have been recorded from few localities although two, *G. prolasius*, from 363 to 1000 m and *C. leptanilla*, 22 to 800 m, cover a wide depth range.

*Bathygnathia vollenhovia*, reported from 800 m, is the only species recorded from both sides of the Tasman Sea. The limited number of specimens of this species from the west coast of New Zealand are not distinguishable from those from the Australian eastern slope. More specimens are needed from both sides of the Tasman Sea to clarify the relationship between the Australian and New Zealand groups.

Only one species, *B. opsithopsis*, has been recorded below 2000 m in Australia and gnathiids are noticeably absent from the limited number of samples taken below this depth (Poore et al., 1994) and rare in other parts of the world. Only *Bythognathia yucatanensis* Camp from 3700–3800 m in the Caribbean, *Caecognathia caeca* Richardson from 2638 m in the western North Atlantic, and *Bathygnathia segonzaci* (Cals) from abyssal depths in the southern Atlantic have been reported from bathyal depths (Camp, 1988).

## **Gnathiidae** Leach

Gnathides Leach, 1814: 432.

Gnathiidae. — Harger, 1880: 408. — Monod, 1926: 281–285 (synonymy) (and other authors)

*Diagnosis*. Pereopods 1 modified as pylopods which lie under buccal cavity. Pereonite 7 reduced, as wide as pleon. Pereopods 7 absent.

Pleon narrower than pereon. Sexually dimorphic. Male head fused to first pereonite; mandible in male large and projecting foward, visible dorsally. Female and praniza larva with pereonites 4–6 fused, inflated. Praniza ectoparasitic on fish.

**Key to genera of Gnathiidae**

The key applies only to adult males and is written for ease of identification; it does not reflect the phylogenetic hypothesis.

1. Pylopod large, distinct; maxilliped 5-articled ..... 2
— Pylopod very thin and elongate (difficult to see even under dissecting microscope), pereopod-like; maxilliped absent or greatly reduced ..... 9
2. Pylopod of 5 or 6 articles; article 3 not reduced ..... 3
— Pylopod of 2 or 3 articles; article 3 reduced or absent ..... 7
3. Frontal border with processes, transverse; pronounced paraoccular ornamentation present ..... *Euneognathia*
— Frontal border without processes, rounded or produced; lacking paraoccular ornamentation ..... 4
4. Pylopod pereopod-like, not operculate; pereonite 1 greatly produced ..... *Bythognathia*
— Pylopod operculate, not pediform; pereonite 1 not greatly produced ... 5
5. Pylopod 6-articled, article 2 reduced; mandibular blade dentate; animal small, < 5 mm ..... *Paragnathia*
— Pylopod 5-articled, article 2 greatly enlarged; mandibular blade smooth or absent; animal large, > 5 mm ..... 6
6. Mandibles without blade; buccal cavity wall extension visible at the end of pronounced rostrum ..... *Bathygnathia*
— Mandibular blade smooth; frontal border rounded, without buccal cavity wall protrusion; pereopod 4 basis with quadratic lobe ..... *Monodgnathia*
7. Frontal border without frontal process, often rounded; cephalon lacking paraoccular ornamentation and dorsal sulcus ..... *Caecognathia*
— Frontal border with frontal processes, often transverse; cephalon may possess paraoccular ornamentation and/or a dorsal sulcus ..... 8
8. Frontal border not deeply excavated, mandibles not elongate ....*Gnathia*
— Frontal border excavated; mandibles long, lacking a dentate blade ..... *Elaphognathia*
9. Pereon smooth, oval; pereonite 7 not visible; pleon often folded under pereon and antennae curved under mandibles; mandibles with crenulate blade and incisor ..... *Thaumastognathia*
— Pereon covered in granules and setae, rectangular; large dorsal, anteriorly-directed projection from pereonite 3; pereonite 7 visible, small; mandibles with highly reduced or absent blade, incisor absent ..... *Gibbagnathia*

**Bathygnathia** Dollfus

*Bathygnathia* Dollfus, 1901: 240. — Monod, 1926: 319.

*Akidognathia* Stebbing, 1913: 12. — Monod, 1926: 289 (type species: *Akidognathia oedipus* Stebbing, 1913).

*Type species. Anceus bathybius* Beddard, 1886 (original designation).

*Diagnosis.* Eyes absent or present. Frontal border produced as rostrum, often long; without processes; buccal cavity wall visible anterodorsally. Mandibles straight, without blade. Pereonite 1 reaching lateral margins of pereon, not immersed in cephalon. Pylopod 5-articled; operculate, second article enlarged; article 3 with 1 or 2 spiniform setae; external margin lacking dense cover of plumose setae. Pereopod 4 basis without anterior quadrate lobe, ischium distally expanded or not; merus of pereopods laterally expanded in some species.

*Remarks. Bathygnathia* is characterised by a 5-articled, operculate pylopod, mandibles without obvious blade and the protruding rostrum and buccal cavity wall. Phylogenetic analysis separated the known species of *Akidognathia* into two groups. The first, including its type species, *A. oedipus*, belongs in a clade with species of *Bathygnathia* and is the sister taxon to the second clade. *Akidognathia* is therefore a junior synonym of *Bathygnathia* and a new genus, *Monodgnathia*, is needed for the second clade.

*A. segonzaci* Cals is very tenatively placed in *Bathygnathia* because of the shape of the mandible and the lack of a quadratic lobe on pereopod 4 but the description of this species is very brief and only the ventral surface was figured.

There are 12 species identified in the literature (Table 4) all confined to the deep sea at depths between 245 and 2698 m. The five newly described species of *Bathygnathia* are the first records of this genus from Australasian waters.

**Key to males of *Bathygnathia* from Australia and New Zealand**

1. Eyes present ..... *B. adlerzia*
— Eyes absent ..... 2
2. Rostrum elongate, two-thirds length of cephalosome and narrow, one third width of cephalosome; pereopod 4 ischium not dilated distally ..... *B. vollenhovia*
— Rostrum rather broad, not elongate; pereopod 4 ischium dilated distally ..... 3
3. Pereonites 1–4 with ornate margins, raised distally; cephalon covered with numerous granules ..... *B. cardiocondyla*
— Cephalon and pereonites 1–4 relatively smooth ..... 4
4. Mandibles indurate, with pronounced incisor; rostrum and cephalon without diamond-shaped translucent region ..... *B. opisthopsis*
— Mandibles thin and flexible in preserved material, without incisor; diamond-shaped translucent region on anterior cephalon ..... *B. tapinoma*

***Bathygnathia adlerzia*** sp. nov.

Figures 4–6

*Material examined.* Holotype. North-western Coral Sea (10°32.1′S, 144°12.1′E), 780–795 m, epibenthic sled, ORV *Franklin*, 20 August 1988 (AM stn 06/88 site 3), AM P41294 (1 male).

Paratype. Type locality, AM P42273 (1 male).

Other material. Western Coral Sea (17°35′S, 146°53′E), 458–500 m, epibenthic sled, M. Pichon et al. on RV *Cidaris*, 15 Jun 1986 (stn 142.2), QM W19964 (1 male, anterior half only).

*Description.* Total length of holotype: 7.82 mm.

Cephalosome pentagonal, 1.4 times as long as wide, lateral margins convex. Rostrum wide and produced with ventrolateral walls of buccal cavity protruding. Holotype very heavily crystallised, no obvious remnants of setae visible on rostrum, rostrum badly torn. Eyes well developed, lateral, sessile and pale. External scissura smoothly rounded. Cephalosome long, one-third length of animal; with broad dorsal sulcus and low, posterior median tubercle. Antenna 1 peduncle article 2 with a large plumose seta distally; flagellum of 5 articles, with 1 aesthetasc. Antenna 2 peduncle twice as long as peduncle of antenna 1; flagellum incomplete, only three articles present. Mandible curved around rostrum, one-third length of cephalosome, cylindrical, lacking obvious blade, with unarmed carina; seta one-third way along; slight mandibular inci-

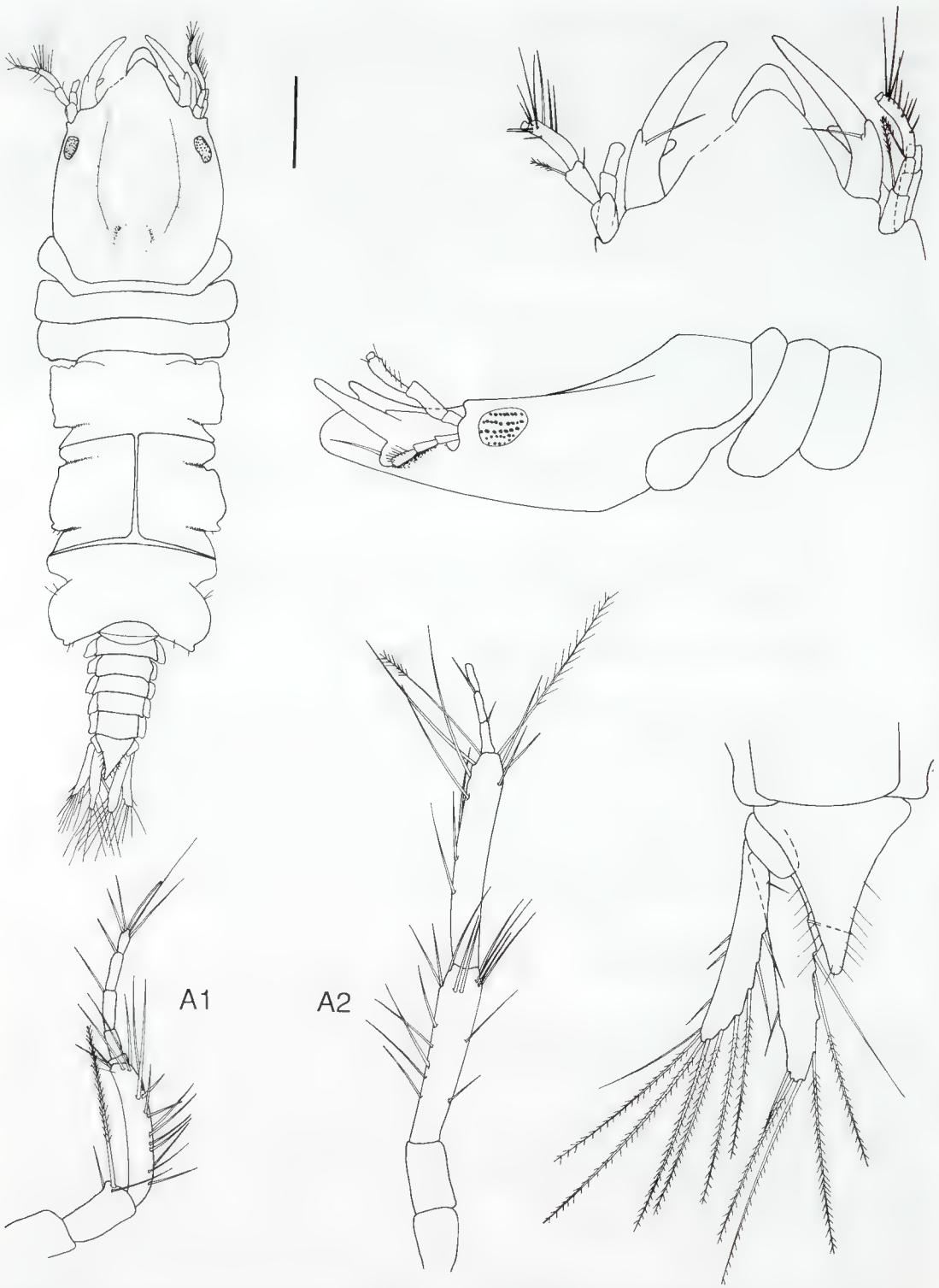


Figure 4. *Bathygnathia adlerzia.* Holotype, AM P41294; A2 of paratype, AM P42180.

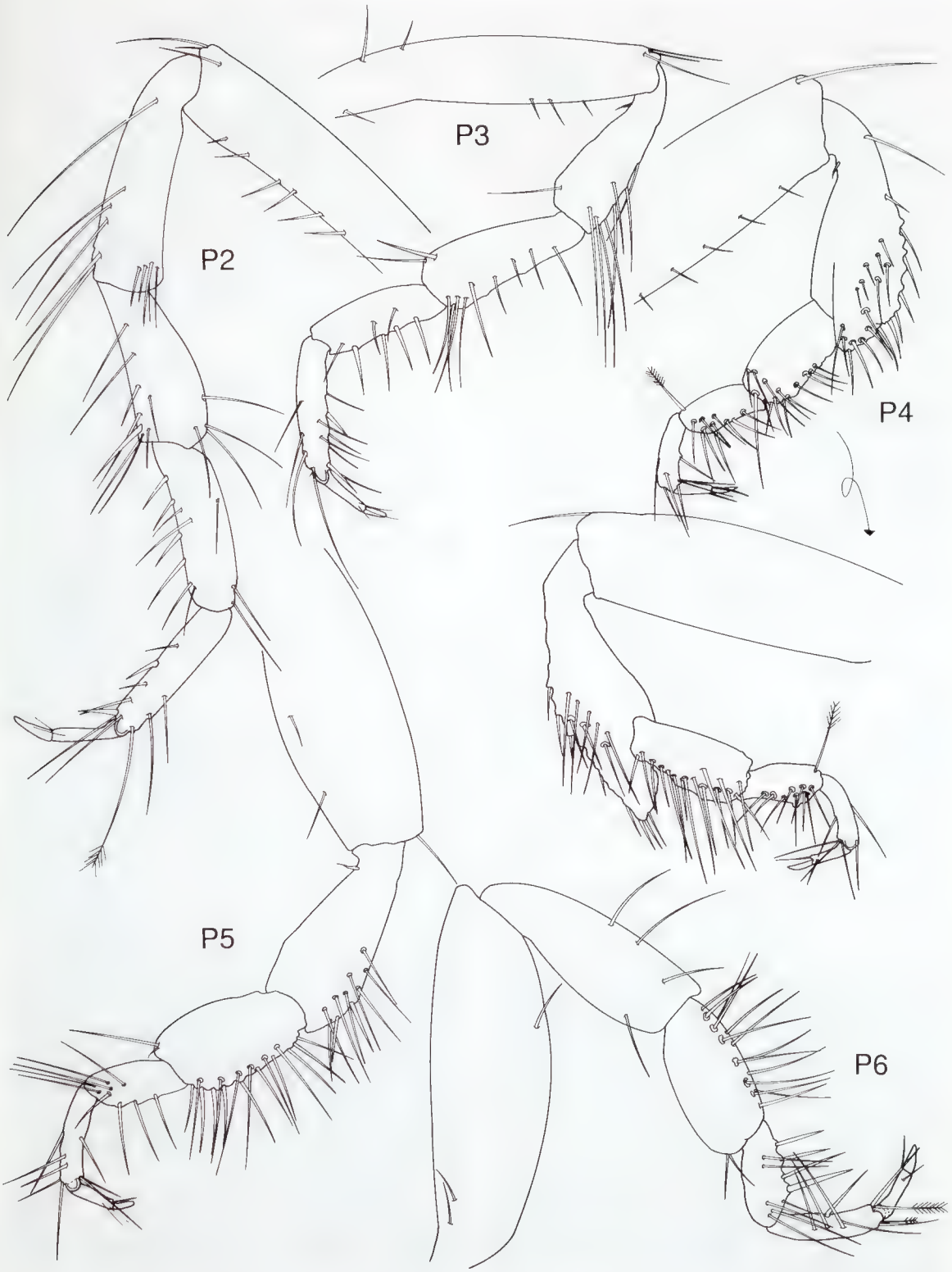


Figure 5. *Bathygnathia adlerzia.* Holotype, AM P41294; P2 of paratype, AM P42180.

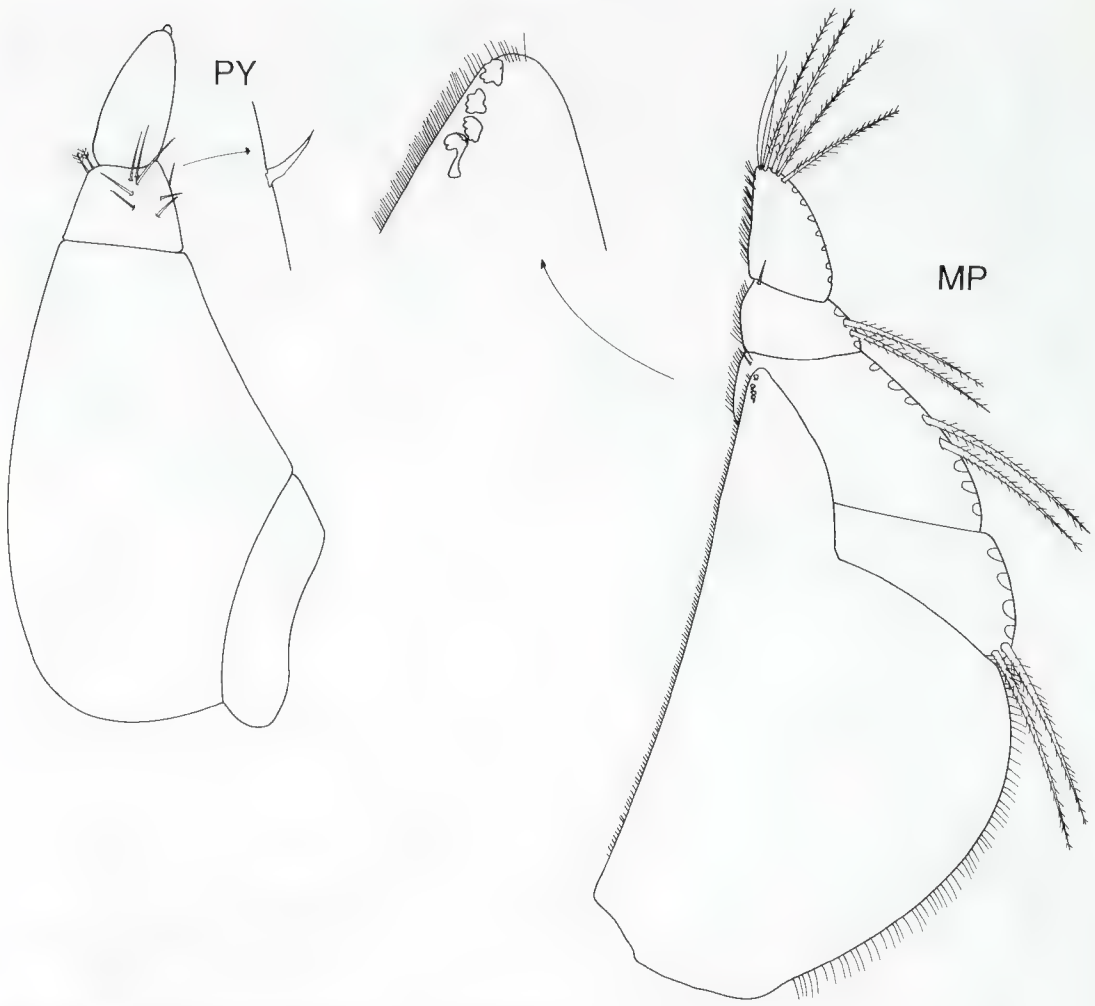


Figure 6. *Bathygnathia adlerzia.* Holotype, AM P41294.

sor near base of seta; 1 conical internal lobe ventrally opposite seta. Maxilliped 5-articled; external margins of articles 2 to 4 bearing plumose setae; endite clearly reaching article 3, wide, with 4 coupling hooks. Pylopod 5-articled: article 1 elongate, firmly attached to article 2; article 3 with 1 spiniform seta on external anterolateral margin and 7 simple setae medianly on ventral surface; article 5 minute.

Pereon widest anteriorly, slightly wider than cephalosome. Pereonite 1 large, laterally directed forward; dorsally reaching lateral margins and laterally visible as one continuous band. Pereonites 2 and 3 subequal, as wide as pereonite 1. Pereonite 4 narrow, with anterior constriction. Pereonite 5 with dorsal sulcus as thin median groove, twice as long as pereonites 2 and 3. Pereonite 6 with small lobuii. Pereonite 7 very narrow, overlapping pleon. Pleonites progressively longer and narrower, pleonal epimera prominent. Pleotelson subtriangular, longer than wide, with 7-8 pairs of simple setae laterally. Uropodal peduncle without setae; rami subequal, reaching well beyond the apex of pleotelson; internal margins of rami bearing numerous plumose setae.

Pereopods with many posterior spiniform setae, particularly on carpus and with dense cover of simple setae; bases of pereopods 2 and 3 narrower than bases of pereopods 4-6; pereopod 4 ischium distally produced.

Pleopods setose. Pleopod 2 endopod with

appendix masculina one-quarter length of rami. Penes 2 contiguous papillae.

*Distribution.* Western Coral Sea, 458–795 m depth.

*Remarks. Bathygnathia adlerzia* is only the second species of *Bathygnathia* described with functional eyes and as such, it is easily separated from all others species except *B. magnifica* Moreira from Brazil. It differs from *B. magnifica* by having a shorter rostrum, mandibles with marked incisors and pereopod 5 lacking a distal expansion of the ischium.

### ***Bathygnathia cardiocondyla*** sp. nov.

Figures 7–9

*Material examined.* Holotype. Eastern Bass Strait, 47 km S of Cape Conran, Vic. (38°24.5′S, 148°42.1′E), 1200 m, sand-silt-clay, pipe dredge, R.S. Wilson on RV *Tangaroa*, 15 Nov 1981 (stn BSS 632) NMV J8372 (1 male).

Paratype. Eastern Bass Strait, 121 km S of Cape Conran, (38°55.6′S, 148°46.4′E), 1730 m, silty clay, pipe dredge, R.S. Wilson on RV *Tangaroa*, 16 Nov 1981 (stn BSS 635) NMV J8371 (1 male).

Other material. New South Wales. East of Terrigal (33°26′S, 152°11′E), 868 m, sled-dredge, FV *Kapala*, 6 Dec 1979, (AM stn K79-20-12), AM P42099 (1 male).

*Description.* Total length of holotype: 6.85 mm.

Cephalosome pentagonal, as long as wide, lateral margins slightly convex. Eyes absent. Frontal border produced as broad rostrum; pointed, with 30 setae submarginally. Anterior margin of rostrum raised; buccal cavity wall visible anteriorly (particularly on paratype). Supraocular lobe smoothly convex. Cephalosome covered with numerous granules; broad dorsal sulcus in distal half and small posterior tubercle. Region between dorsal sulcus and frontal margin of rostrum translucent. Antenna 1 flagellum of 5 articles, with 2 aesthetascs. Antenna 2 longer than antenna 1; flagellum of 6 articles (possibly some flagellum articles missing). Mandible half length of cephalosome, cylindrical with narrow apex; a slightly armed carina; pronounced proximal mandibular incisor; mandibular seta one-quarter way along; conical internal lobe ventrally opposite incisor. Maxilliped 5-articled; external margins of articles 2 to 4 bearing plumose setae; endite clearly reaching article 3, with 5 coupling hooks. Pylopod 5-articled: article 3 with 2 pectinate setae on external anterolateral margin; articles 2–4 with 13 setae medianly; article 5 minute.

Pereon evenly sided, as wide as cephalosome except pereonite 5 which is wider around base of pereopods. Pereonite 1 dorsally raised forming saddle-like structure with pereonite 2 laterally; dorsally small, not reaching lateral margins of pereon and partially obscured laterally by pereonite 2. Pereonites 1–4 with granular ornate borders. Pereonite 4 with raised ornate ridge near posterior border. Pereonites 2 and 3 much shorter than 4–6, pereonite 5 longest. Pereonite 6 lobuii thin and elongate. Pereonite 7 small, very narrow, overlapping pleon. Pleonites progressively narrower, pleonal epimera prominent. Pleotelson subtriangular, tapering, as wide as long; lateral margins sinuous with 3 pairs of simple setae laterally. Uropodal peduncle with 2 setae; rami subequal, reaching beyond apex of pleotelson, internal margins bearing numerous plumose setae.

Pereopods with dense cover of simple setae particularly on basis; pereopod 2 with 1 posterior spiniform seta on carpus; pereopod 4 with numerous tubercles, carpus wide and ischium with anterodistal projection.

Pleopods setose. Pleopod 2 endopod with appendix masculina subequal to rami. Penes 2 contiguous papillae.

*Distribution.* Southern NSW, eastern Bass Strait, 868–1730 m depth.

*Remarks. Bathygnathia cardiocondyla* is easily identified and separated from all other *Bathygnathia.* The raised and ornate appearance of the edges of the cephalon and pereonites 1–4 is unique amongst the *Bathygnathia* but similar in some ways to *Bythognathia yucatanensis* Camp.

### ***Bathygnathia opisthopsis*** sp. nov.

Figures 10–12

*Material examined.* Holotype. New South Wales, E of Newcastle, (33°03.6′S, 152°48′E), 2632–2698 m, Menzies trawl, W. Ponder and R.T. Springthorpe, 8 Oct 1982 (AM stn U216), AM P42181 (1 male).

Paratype. Type locality, AM P42105 (1 male).

*Description.* Total length of holotype: 7.67 mm.

Cephalosome pentagonal, as long as wide, lateral margins slightly convex. Eyes absent. Frontal border produced as broad rostrum; pointed and raised, with few submarginal setae. Buccal cavity wall clearly visible beyond anterior margin of rostrum. Supraocular lobe smoothly convex. Cephalosome smooth; with

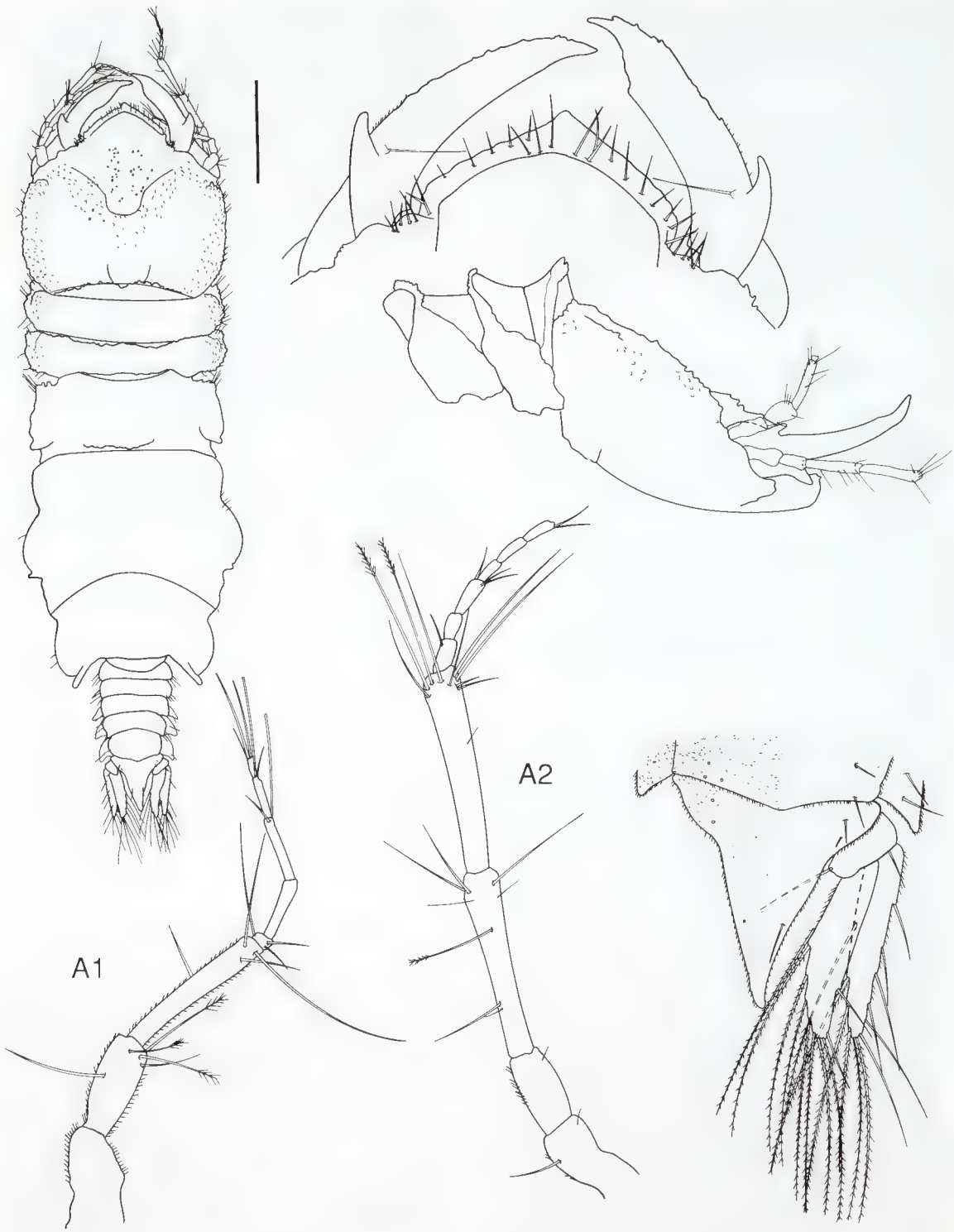


Figure 7. *Bathygnathia cardiocondyla*. Holotype, NMV J8372.

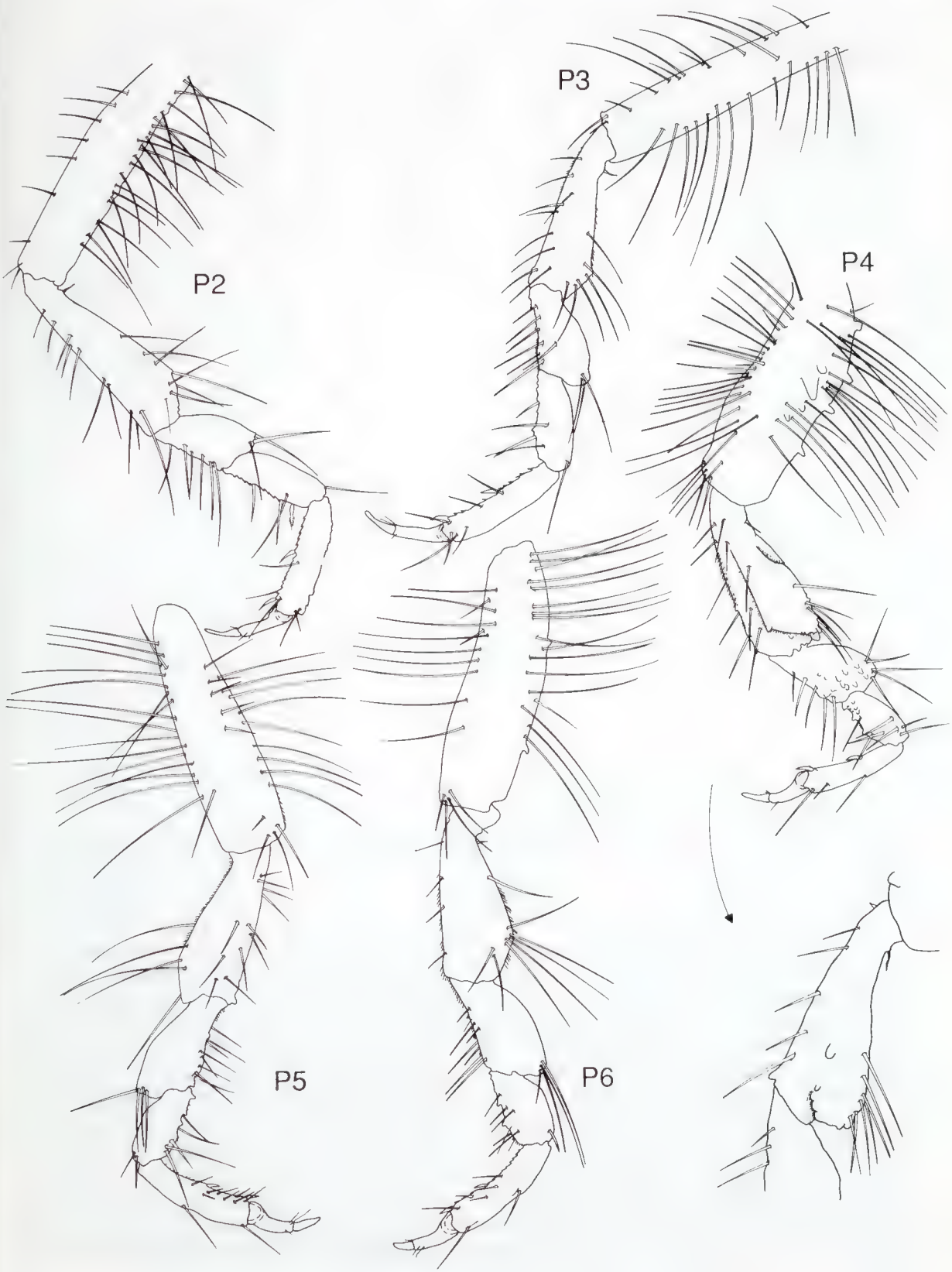


Figure 8. *Bathygnathia cardiocondyla*. Holotype, NMV J8372.

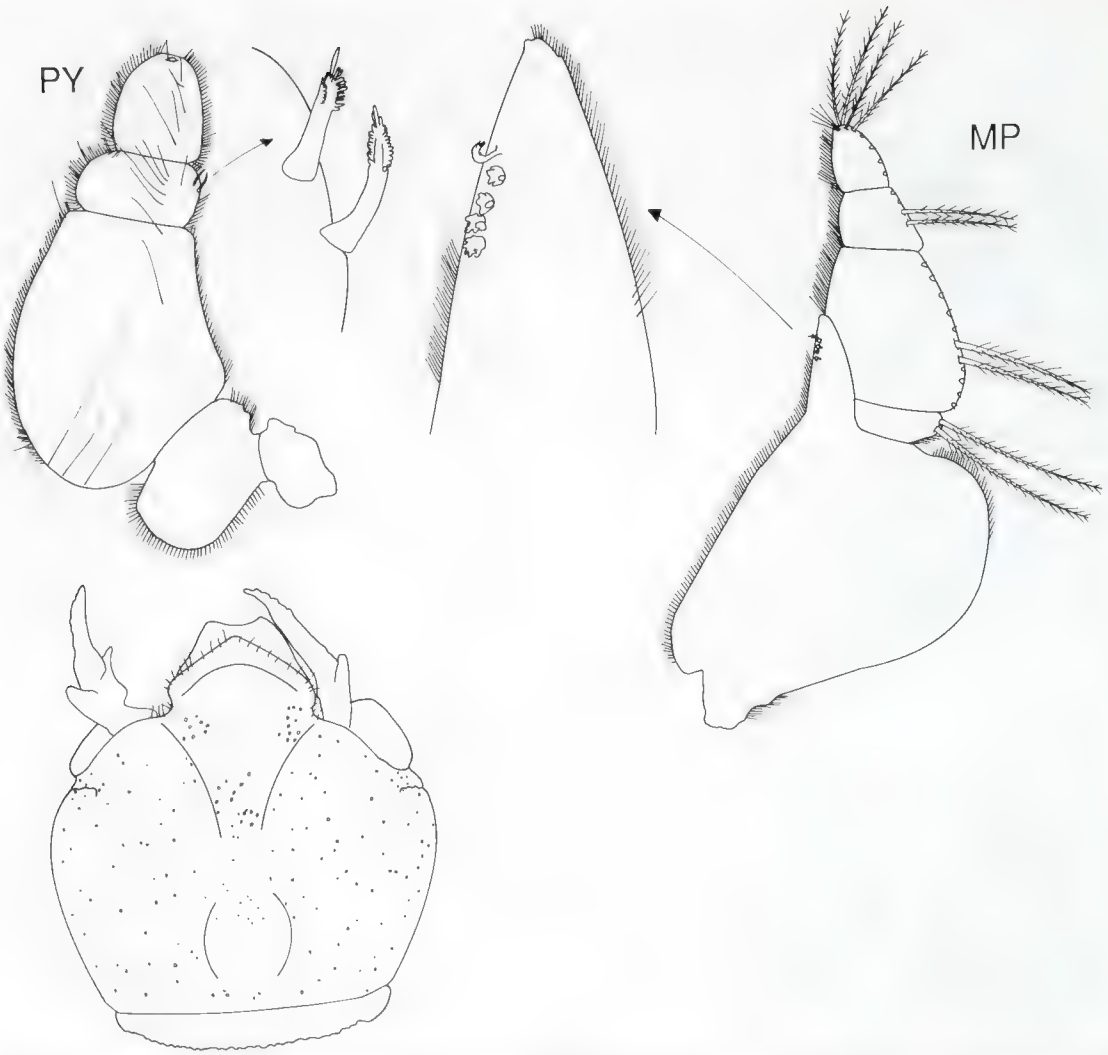


Figure 9. *Bathygnathia cardiocondyla*. Holotype, NMV J8372; Dorsal view of cephalon paratype, AM P42099.

broad but shallow dorsal sulcus extending posteriorly to base of posterior median tubercle. Antenna 1 flagellum of 5 articles, with no aesthetasc. Antenna 2 twice as long as antenna 1; flagellum of 8 articles. Mandible half length of cephalosome, cylindrical with tapered apex; armed carina extending to distal apex of mandible; pronounced mandibular incisor and conical internal lobe ventrally, opposite incisor. Maxilliped 5-articled; external margins of articles 2 to 4 bearing plumose setae; endite clearly reaching article 3, with 3 coupling hooks. Pylopod 5-articled: article 2 with 1 large aerola; article 3 with 2 strong setae on external anterolateral margin; articles 2–3 with few short setae on ventral surface; article 5 minute.

Pereon evenly sided, as wide as cephalosome except pereonite 5 which is slightly wider around base of pereopods. Pereonite 1 narrow, clearly reaching lateral margins of pereon dorsally and visible laterally. Pereonites 2 and 3 much shorter than each of pereonites 4–6, pereonite 5 longest. Pereonite 6 lobuii thin and elongate. Pereonite 7 small, overlapping narrow pleon. Pleonites progressively narrower, pleonal epimera not prominent. Pleotelson damaged; subtriangular, with rounded apex; wider than long; lateral margins sinuous with up to 4 pairs of simple, short setae

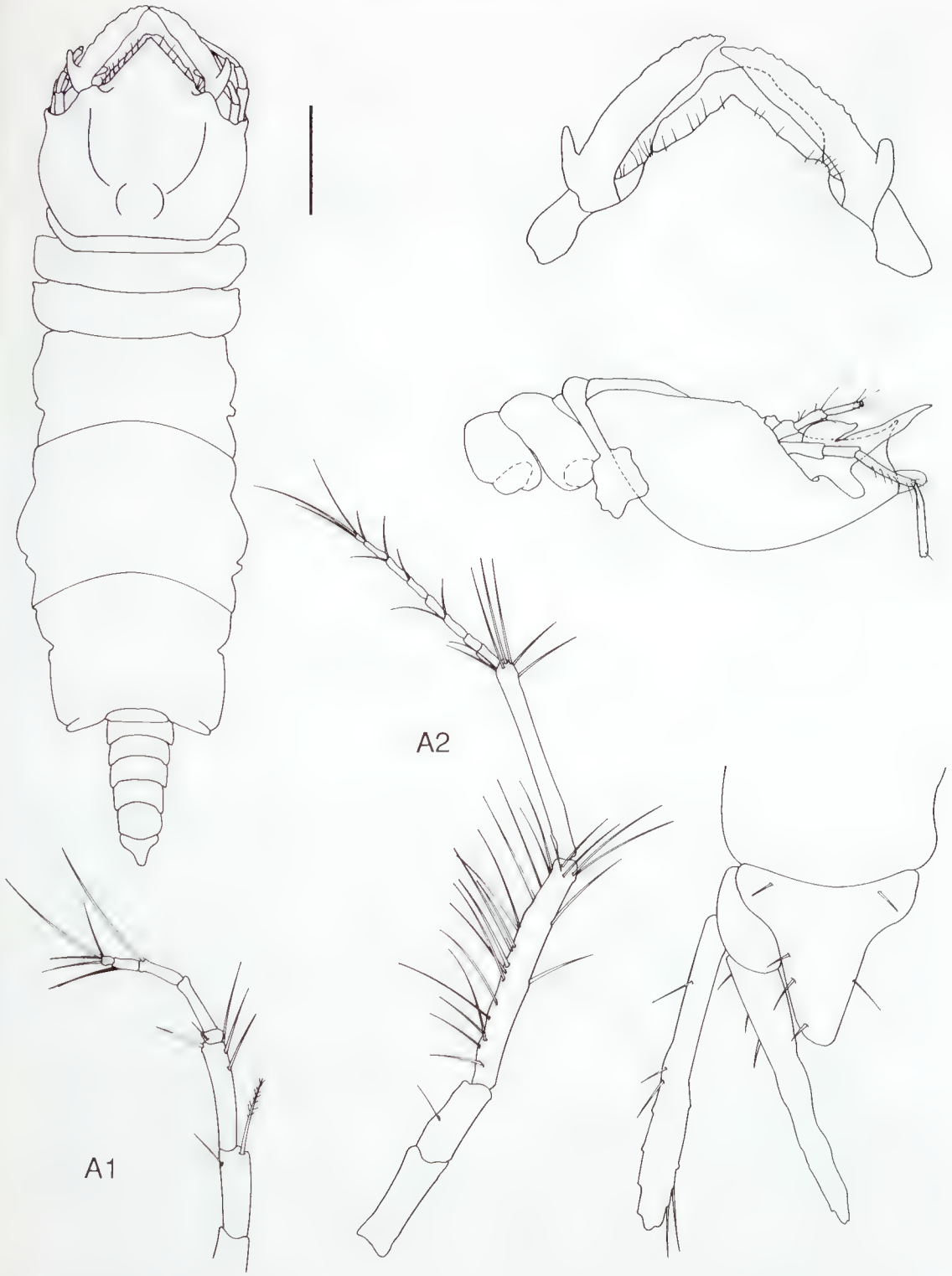


Figure 10. *Bathygnathia opisthopsis*. Holotype, AM P42181.

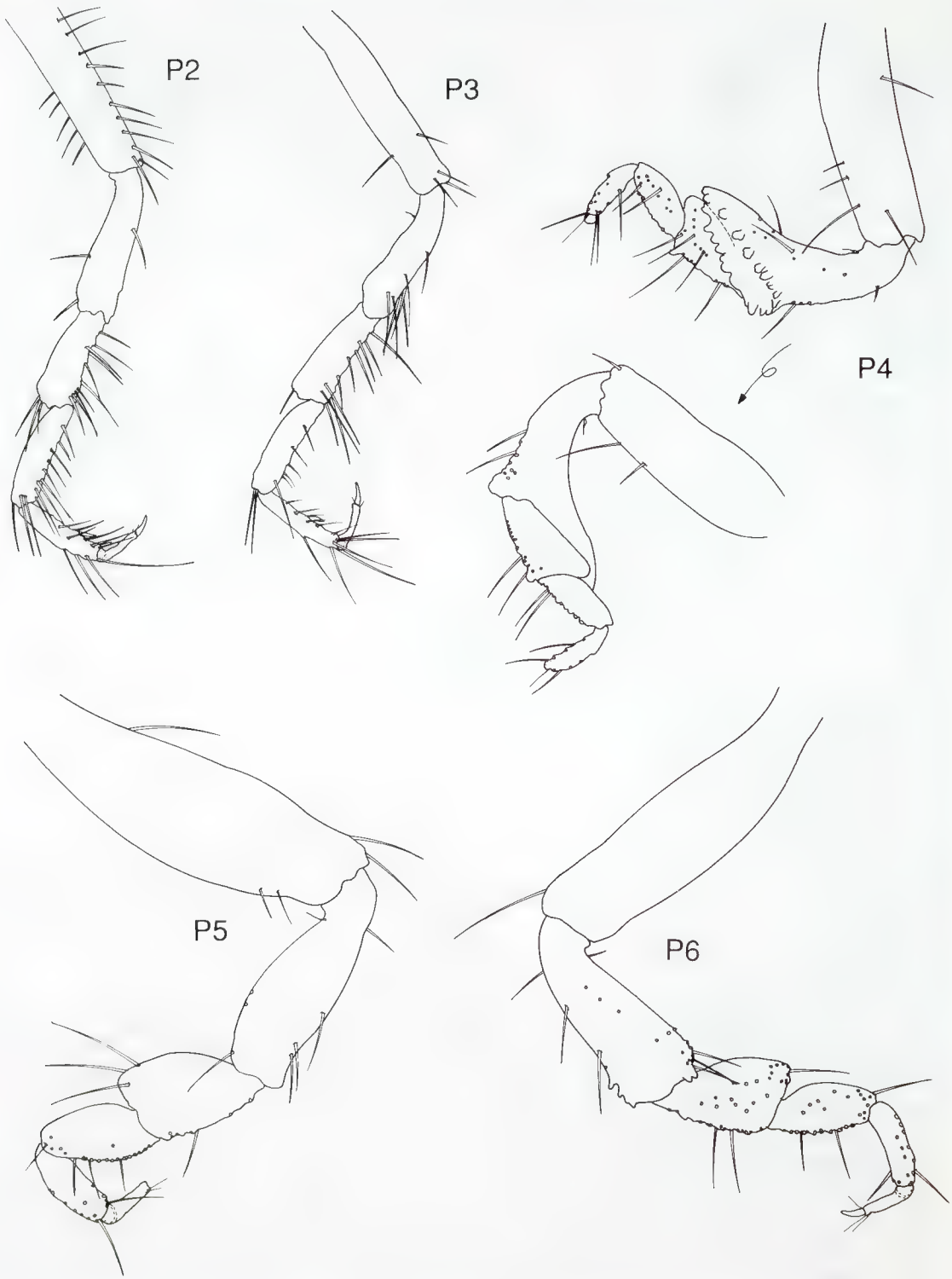


Figure 11. *Bathygnathia opisthopsis*. Holotype, AM P42181; P5 and P6 of paratype, AM P42105.

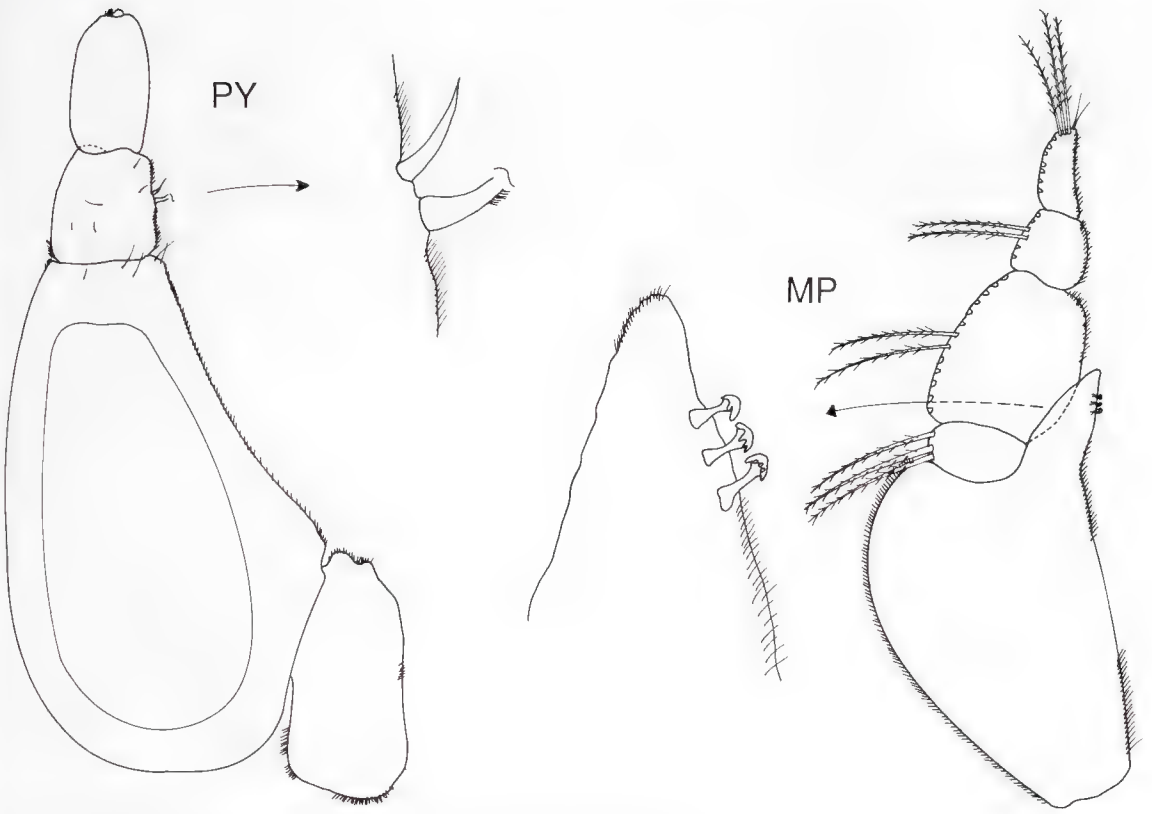


Figure 12. *Bathygnathia opisthopsis*. Holotype, AM P42181.

laterally. Uropodal peduncle without setae; rami subequal, long and narrow, reaching well beyond apex of pleotelson, external margins bearing numerous setae.

Pereopods with dense cover of simple setae particularly distally; pereopods 2 and 3 less stout than pereopods 4–6; ischium of pereopod 4 with very pronounced anterodistal projection, distally flattened with numerous small tubercles.

Pleopods setose. Pleopod 2 endopod with appendix masculina three-quarters or almost as long as rami. Penes 2 contiguous papillae.

*Distribution.* Southern NSW, 2632–2698 m.

*Remarks. Bathygnathia opisthopsis* possesses similar body proportions and similar mandibles to those of *B. cardiocondyla* but lacks the raised and ornate margins of the anterior pereonites. Both species are characterised by the weakly armed mandibular carina. *B. opisthopsis* was collected almost 1000 m deeper than any other specimen of *Bathygnathia.*

***Bathygnathia tapinoma*** sp. nov.

Figures 13–15

*Material examined.* Holotype. New Zealand. Off W coast of South Island (42°15.9′S, 170°1.8′E), 924 m, letter-box dredge, P.K. Probert, 17 Feb 1982 (NZOI stn Q689A), NZOI H-618 (1 male).

Paratype. Type locality, NMV J4753 (2 males).

Other material. Type locality, NMV J4755 (1 female).

*Description.* Total length of holotype: 5.39 mm.

Cephalosome pentagonal, 1.4 times as long as wide, lateral margins convex. Entire frontal border produced as very wide rostrum with many setae on anterior margin; ventrolateral walls of buccal cavity protruding considerably beyond rostrum. Cephalosome with large, diamond-shaped translucent region on rostrum. Eyes absent. External scissura smoothly rounded. Antenna 1 flagellum of 5 articles, with 3 aesthetascs; antenna 2 longer than antenna 1; flagellum

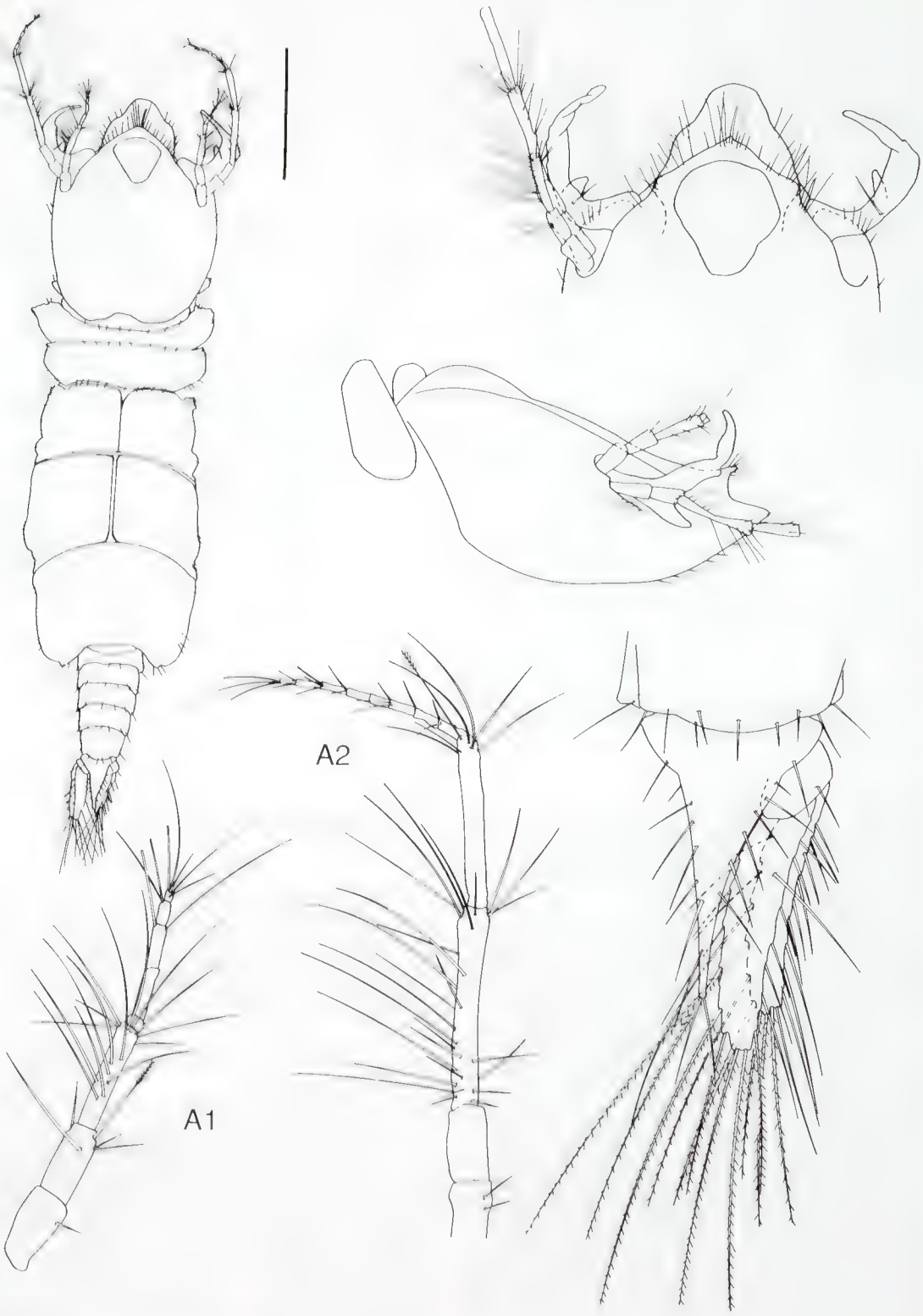


Figure 13. *Bathygnathia tapinoma*. Holotype, NZOI H-618.

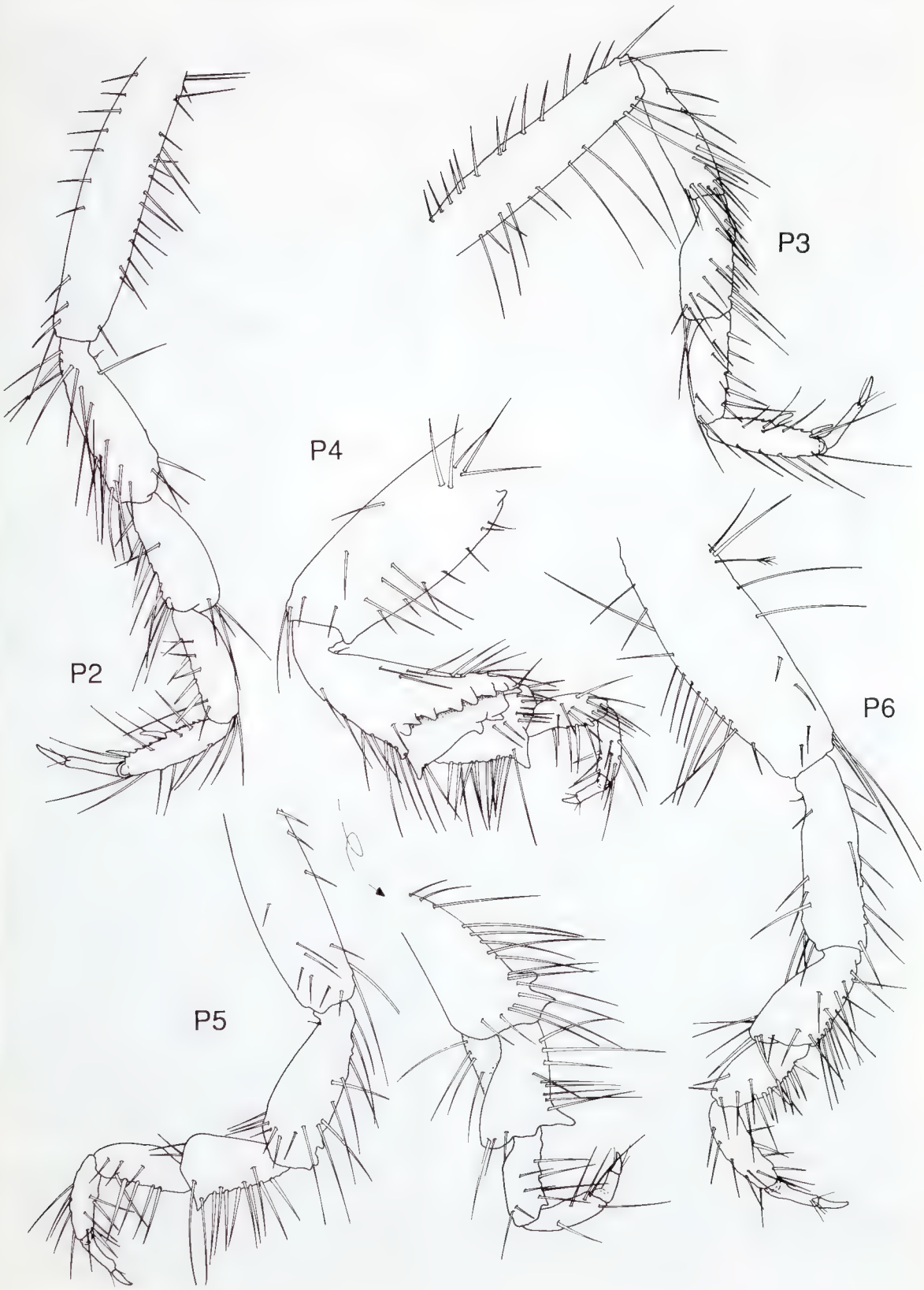


Figure 14. *Bathygnathia tapinoma*. Holotype, NZOI H-618.

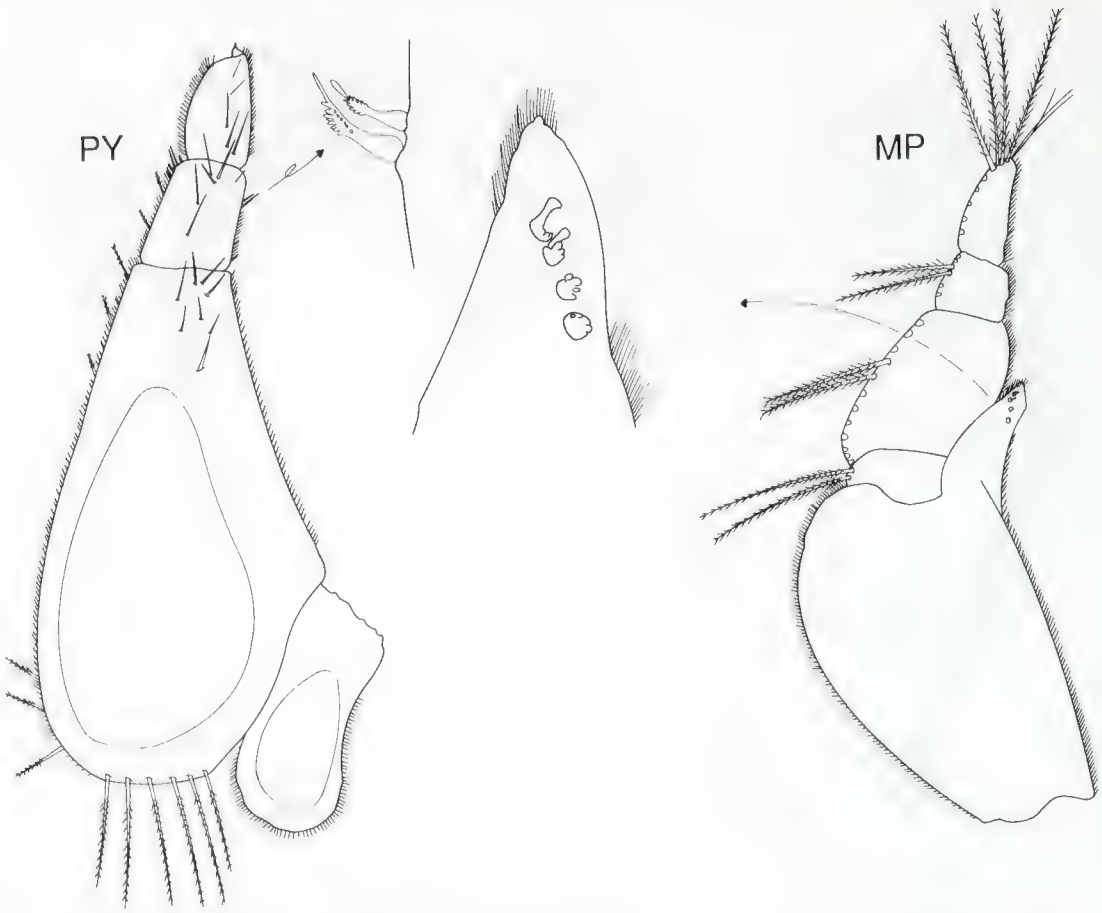


Figure 15. *Bathygnathia tapinoma*. Holotype, NZOI H-618.

of 8 articles. Mandible soft and flexible in preserved specimens; one-third length of cephalosome; distally raised in lateral view; apex curved inwards; cylindrical, with no recognisable blade; a unarmed carina; seta one-third way along; inferior conical internal lobe distal to seta. Maxilliped 5-articled; external margins of articles 2 to 4 bearing plumose setae; endite clearly reaching article 3, with 4 coupling hooks. Pylopod 5-articled; internal margin with few well-spaced long plumose setae proximally and short plumose setae distally; anteromedianly with numerous simple setae; article 1 elongate, firmly attached to article 2; articles 1 and 2 with areolae; article 3 with 2 pectinate setae on external anterolateral margin; fifth article minute.

Pereon widest at pereonite 2, slightly wider than cephalosome; pereonites progressively longer. Pereonite 1 dorsally reaching lateral margins, divided into 3 regions by cephalon and partially obscured laterally by pereonite 2. Pereonite 3 narrowest, pereonites 4–6 progressively wider. Pereonite 4 with anterior constriction and thin median groove. Pereonite 5 with dorsal sulcus as thin median groove. Pereonite 6 with very small lobuii. Pereonite 7 very narrow, overlapping pleon. Pleonites progressively longer and narrower, pleonal epimera not prominent. Pleotelson subtriangular, longer than wide; lateral margins straight; with 7–8 pairs of simple setae laterally and pair of seta on distal apex. Uropodal peduncle with 1 seta; endopod longer than exopod, reaching beyond apex of pleotelson; internal margins of rami bearing numerous plumose setae.

Pereopods with many posterior setae and dense cover of simple setae; pereopods 2 and 3 less robust than 4 to 6; pereopod 4 basis without quadrate lobe, ischium distally expanded as concave circular cusp with 10 or more tubercles.

Pleopods setose. Pleopod 2 endopod with appendix masculina three-quarters length of rami. Penes 2 contiguous papillae.

*Distribution.* West coast of South Island of New Zealand, 924 m.

*Remarks. Bathygnathia tapinoma* is most similar to *B. oedipus* (Stebbing) and both are characterised by the presence of a pronounced distal extension on the ischium of pereopod 4; weak mandibles located closer to the lateral margin on the frontal border than in most other species; and similar pereon and pleotelson dimensions. *B. tapinoma* differs from *B. oedipus* in possessing a wider yet shorter rostrum and a large diamond-shaped translucent region at the base of the rostrum.

***Bathygnathia vollenhovia*** sp. nov.

Figures 16–18

*Material examined.* Holotype. Tasmania, off Freycinet Peninsula (42°2.20′S, 148°38.70′E), 800 m, coarse shelly sand, WHOI epibenthic sled, M.F. Gomon et al. on ORV *Franklin*, 27 Jul 1986 (stn SLOPE 45), NMV J19120 (1 male).

Other material. New Zealand, off W coast of South Island, (42°15.9′S, 170°1.8′E), 924m, letter-box dredge, P.K. Probert, 17 Feb 1982 (NZOI stn Q689A), NMV J4754 (1 male).

*Description.* Total length of holotype: 9.66 mm.

Cephalosome pentagonal, 1.4 times as long as wide, lateral margins convex. Rostrum narrow and greatly produced; half length of cephalon; at base approximately one-third width of cephalosome; with many short setae on anterior margin. Ventrolateral walls of buccal cavity protruding anteriorly; cephalon with translucent elliptical region on rostrum (faded in some material). Eyes absent. External scissura smoothly rounded. Supraocular lobe very low, acute. Cephalosome with broad, shallow dorsal sulcus, two-thirds length of cephalon; low, very small posterior median tubercle. Antenna flagellum of antenna 1 of 5 articles, with 4 aesthetases; antenna 2 longer than antenna 1; flagellum of 6 articles. Mandible subequal to length of cephalosome (excluding rostrum); proximal two-thirds slightly curved, distal third with internal margins parallel, forming vice-like structure; with unarmed carina; slight mandibular incisor almost half-way along; lacking seta. Maxilliped 5-articled; external margins of articles 2 to 4 bearing plumose setae; endite clearly reaching article 3, wide, with 5 coupling hooks. Pylopod 5-articled, with many setae medianly on ventral surface; margin of article 2 with several plumose setae; article 3 with 1 pectinate seta on external anterolateral margin; fifth article minute.

Pereon evenly sided, as wide as cephalosome. Pereonite 1 large, laterally directed forward; reaching lateral margins dorsally and visible as continuous band laterally. Pereonite 2 and 3 subequal, shorter than pereonites 4–6. Pereonite 5 with dorsal sulcus as thin median groove. Pereonite 7 very narrow, overlapping pleon. Pleonite 1 wider than other pleonites, pleonal epimera prominent. Pleotelson subtriangular, as wide as long, lateral margins sinuous with 17–18 pairs of simple setae laterally and 3 setae medianly. Uropodal peduncle with 4 setae; endopod longer than exopod, reaching beyond apex of pleotelson; rami bearing numerous plumose setae distally.

Pereopods with dense cover of simple setae and with many strong posterior setae, particularly on carpus; pereopods 4–6 more stout than 2 and 3, with laterally enlarged merus.

Pleopods setose. Pleopod 2 endopod with appendix masculina half length of rami. Penes 2 contiguous papillae.

*Distribution.* Tasman Sea, off west coast of South Island of New Zealand and east coast of Tasmania, 800 m depth.

*Remarks.* Of the blind species, *Bathygnathia vollenhovia* is most similar to *B. bathybius* (Beddard) and *B. monodi* Cals. All possess a long narrow rostrum of similar proportions. These three species, and *B. curvirostris* Richardson, *B. affinis* Birstein and *B. porca* Kensley, form a complex of species characterised by a most pronounced rostrum and expand merus of some or all of pereopods 2–6. *B. vollenhovia* differs from *B. bathybius* in possessing a more complex mandible characterised by incisors and an opposing straight distal region; and from *B. monodi* in a more complex and rounded mandible, shorter translucent elliptical region confined entirely to the rostrum and cephalon with a posterior tubercle and dorsal sulcus.

***Bythognathia*** Camp

*Bythognathia* Camp, 1988: 668.

*Type species. Bythognathia yucatanensis* Camp, 1988 (original designation).

*Diagnosis.* Eyes absent. Frontal border produced into rostrum, without processes. Mandibles straight, lacking obvious blade. Pereonite 1

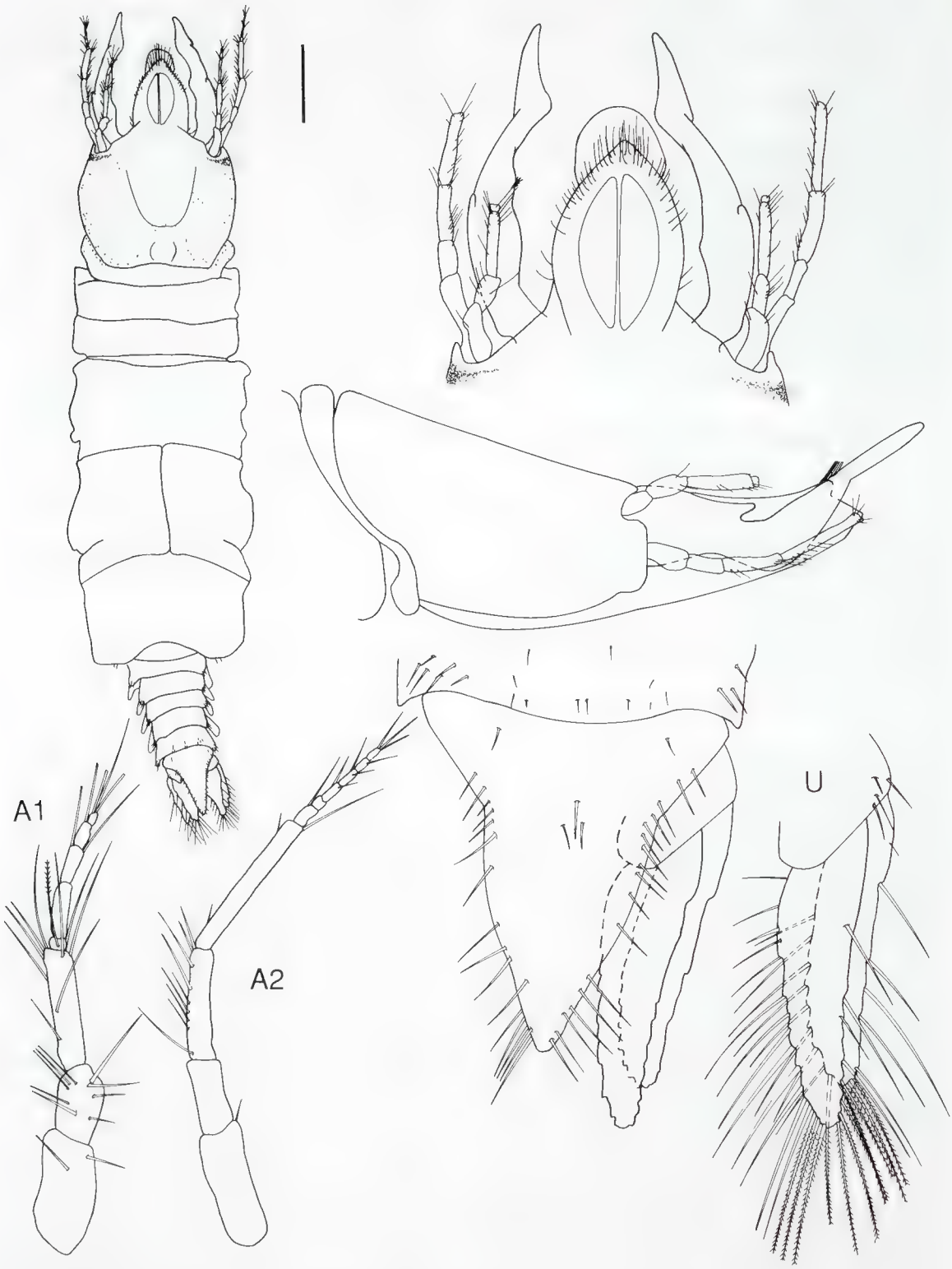


Figure 16. *Bathygnathia vollenhovia.* Holotype, NMV J19120.

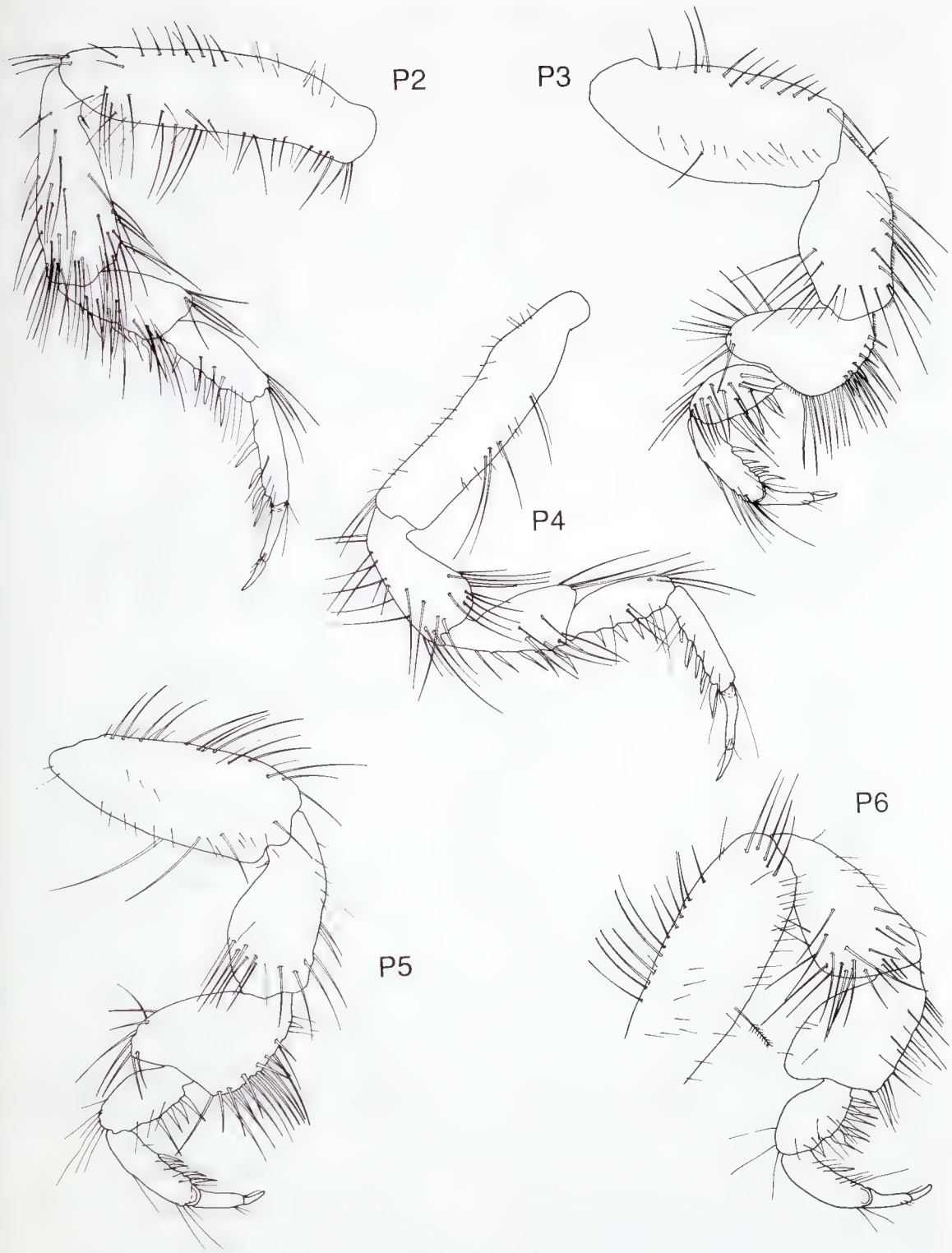


Figure 17. *Bathygnathia vollenhovia*. Holotype, NMV J19120.

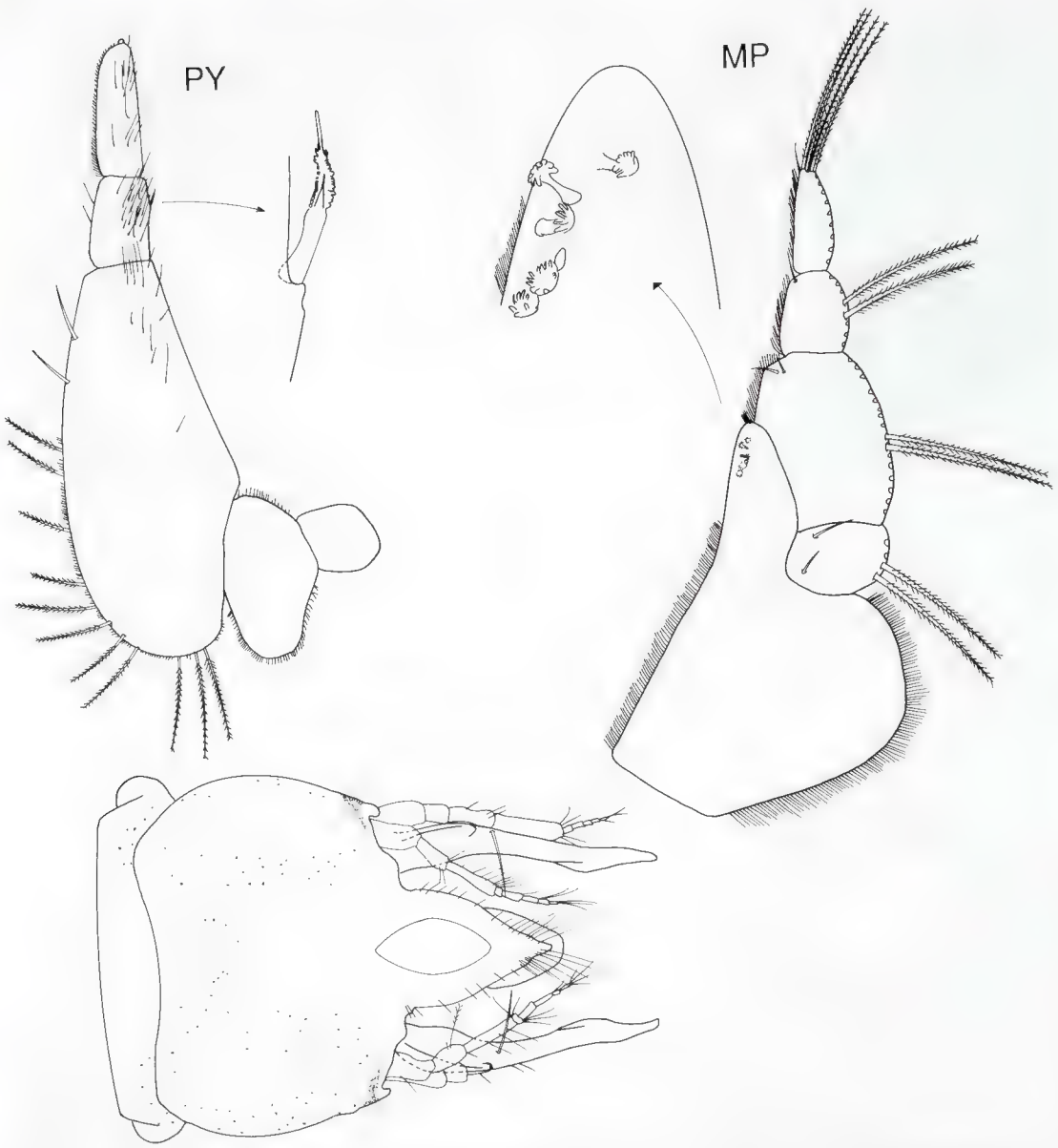


Figure 18. *Bathygnathia vollenhovia*. Holotype, NMV J19120; Dorsal view of cephalon of NMV J4754.

produced, partially obscuring pereonite 2; clearly reaching lateral margins of pereon. Pylopod 6-articled (sixth article fused), not operculate, subchelate and pediform.

*Remarks*. *Bythognathia* is a monotypic genus from very deep water in the Caribbean Sea (Camp, 1988). It is characterised by the very large and produced pereonite 1. *Bythognathia* is the only gnathiid with a 6-articled, non-operculate pylopod which is pediform and subchelate. The phylogenetic analysis supports the retention of the generic name. The genus does not occur in Australia.

### ***Caecognathia*** Dollfus

*Caecognathia* Dollfus, 1901: 240. — Tattersall, 1906: 61.

*Gnathia* (*Perignathia*) Monod, 1922: 645 (type species: *Anceus abyssorum* Sars, 1872 or *Gnathia fallax* Monod, 1926. See *Remarks* under *Gnathia*).

*Heterognathia* Amar and Roman, 1974: 569 (type species: *Heterognathia adeliensis* Amar and Roman, 1974).

not *Gnathia* (*Perignathia*). — Monod, 1926: 554–555.

*Type species. Anceus stygius* Sars, 1877 (original designation).

*Diagnosis.* Eyes present. Frontal margin of cephalon produced, without frontal processes. Mandibles usually with smooth mandibular blade. Cephalon without paraocular ornamentation or dorsal sulcus. Pereonite 1 immersed in cephalon. Pylopod 2- or 3-articled, operculate, article 1 enlarged, article 3 small or absent.

*Remarks.* The type species of *Heterognathia, H. adelaidensis*, is a juvenile male of the common Antarctic species, *Gnathia calva* Vanhöffen (Wägele, 1987) herein transferred to *Caecognathia*. This genus is therefore a junior synonym of *Caecognathia*. The nomenclatural status of *Perignathia* is uncertain but of little consequence as long as it remains a junior synonym; see *Remarks* under *Gnathia*.

*Gnathia* and *Caecognathia* are closely related genera formerly synonymised. They share many similarities, particularly the structure of the pylopod but *Caecognathia* is distinguished by a produced frontal border lacking any frontal processes. The genus includes most species of Monod's (1926) Sectio Productae of *Gnathia*.

The only previously described Australian species assigned to this genus are *C. agwillisi* (Seed, 1979) from rocky shores in Victoria (Fig. 2A) and *C. pustulosa* (Hale, 1924) from sponges in South Australia (Fig. 2B and Table 5).

**Key to males of Australian species of *Caecognathia***

1. Pleotelson trapeziform, apex broadly truncated ..... *C. agwillisi*
— Pleotelson subtriangular ..... 2
2. Cephalosome elliptical; pereon width evenly increasing posteriorly to pereonite 5; pereonite 6 with marked globular lobuii (see figs 19, 22, 34, 40) ..... 3
— Cephalosome roughly quadrilateral; pereon width not steadily increasing posteriorly; pereonite 6 without lobuii or at most with simple, rounded lobuii only ..... 6
3. Rostrum produced ..... *C. leptanilla*
— Rostrum not produced ..... 4
4. Pereonite 6 with pronounced suture midway along lateral margin ..... *C. diacamma*
— Pereonite 6 without suture ..... 5
5. Pereonite 1 barely reaching lateral margins of body; frontal border smoothly rounded with rounded external scissura ..... *C. brachyponera*
— Pereonite 1 clearly reaching lateral margins of body, divided into 3 regions by posterior margin of cephalon; frontal border with a slight median indentation and very shallow external scissura ..... *C. trachymesopus*
6. Cephalon with 3 furrows, 2 mesiolateral and 1 medially; pylopod 2-articled ..... 7
— Cephalon without furrows; pylopod 3-articled ..... 9
7. Mandibles with internal quadrate lobe; pereonite 4 with posterior bilobed projection ..... *C. paratrechia*
— Mandibles lacking internal lobe; pereonite 4 with anterior spine ..... 8
8. Body not setose; mandibles without mandibular setae, blade a smooth arc; cephalon without low tubercle, spine on peronite 4 pronounced ..... *C. pustulosa*

— Body setose, especially anteriorly; mandibles with mandibular setae, blade slightly asssymetrical, produced; posterior cephalon with small tubercle .. ..*C. huberia*

9. Mandibles with armed carina; small opaque spines on cephalon, visible in lateral view; frontal border produced as a rostrum; pereopod 4 basis not produced distally ..... *C. dolichoderus*

— Mandibles cylindrical, without armed carina; no spines on cephalon; frontal border not produced as a rostrum; pereopod 4 basis expanded distally ... ..... *C. gnamptogerys*

***Caecognathia branchyponera*** sp. nov.

Figures 19–21

*Material examined.* Holotype. New South Wales, 44 km E of Nowra (34°55.79′S, 151°08.06′E), 429 m, muddy coarse shell, WHOI epibenthic sled, G.C.B. Poore et al. on RV *Franklin*, 22 Oct 1988 (stn SLOPE 56), NMV J27575 (1 male).

Paratypes. Type locality, NMV J19126 (6 males).

Other material. Type locality, NMV J29889 (4 females). Vic. S of Point Hicks (38°17.70′S, 149°11.30′E), 400 m, coarse sand, gravel, mud, many sponges, WHOI epibenthic sled, M.F. Gomon et al. on RV *Franklin*, 24 Jul 1986 (stn SLOPE 40), NMV J19125 (80 specimens).

*Description.* Total length: 3.09 mm.

Cephalosome elliptical, 1.2 times as long as wide, lateral margins convex. Eyes well developed, lateral and sessile. Frontal border slightly produced, rounded; with 5 submarginal setae each side of mid-dorsal line. External scissura smoothly rounded. Supraocular lobe smoothly convex. Antennae stout, subequal; flagellum of antenna 1 of 5 articles, without aesthetascs; flagellum of antenna 2 of 3 articles. Mandible strongly curved, one-third length of cephalosome; with unarmed carina; smooth double-scalloped blade on distal two-thirds, distal scallop twice as long as proximal scallop; basal neck ventrally smoothly arced, dorsally covered by pronounced erisma. Erisma with dense covering of fine setae on external margin. Maxilliped 5-articled; palp thin and elongate; external margins of articles 2–4 bearing plumose setae; endite clearly reaching article 3, wide. Pylopod 3-articled: internal margin of plumose setae; article 1 with 4 plumose setae on ventral surface; article 2 conical, proximal margin completely joined to article 1, with 3 setae on ventral surface; article 3 minute.

Pereon width increasing posteriorly; widest at pereonite 5, 1.75 times as wide as cephalosome; margins with numerous setae. Pereonite 1 barely reaching lateral margins dorsally and partially obscured laterally by pereonite 2. Pereonites 5 and 6 each twice as long as pereonites 2–4; posterior border of pereonite 6 markedly concave with distinct gobular lobuii. Pereonite 7 very narrow, overlapping pleon. Pleon with pleonites subequal, epimera prominent. Pleotelson subtriangular, longer than wide; lateral margins slightly sinuous; with 3 pairs of plumose setae laterally and pair of setae on distal apex. Uropodal peduncle with 1 plumose seta on internodistal margin; rami subequal, not reaching apex of pleotelson; internal margins of rami bearing numerous plumose setae.

Pereopods with moderate cover of plumose setae, particularly on basis and few, pronounced lateral projections on anterior face of ischium to carpus.

Pleopods setose. Pleopod 2 endopod lacking appendix masculina. Penes 2 small contiguous papillae.

*Distribution.* Eastern Bass Strait, eastern NSW, 400–429 m.

*Remarks. Caecognathia branchyponera* belongs to a complex of species characterised by a roughly elliptical cephalosome; simple mandibles; pear-shaped pereon; presence of globular lobuii; and distinct pylopods (article 2 is not circular). The three species *C. leptanilla*, *C. trachymesopus* and *C. diacamma* also belong to this complex.

*C. branchyponera* most closely resembles *C. trachymesopus* though is distinguishable by the smaller pereonite 1 which is not divided into three regions; a flatter frontal border with evenly spread small setae, a deeper external scissura and no median indentation.

***Caecognathia diacamma*** sp. nov.

Figures 22–24

*Material examined.* Holotype. Victoria, western Bass Strait, 26 km SW of Cape Otway (39°01.0′S,

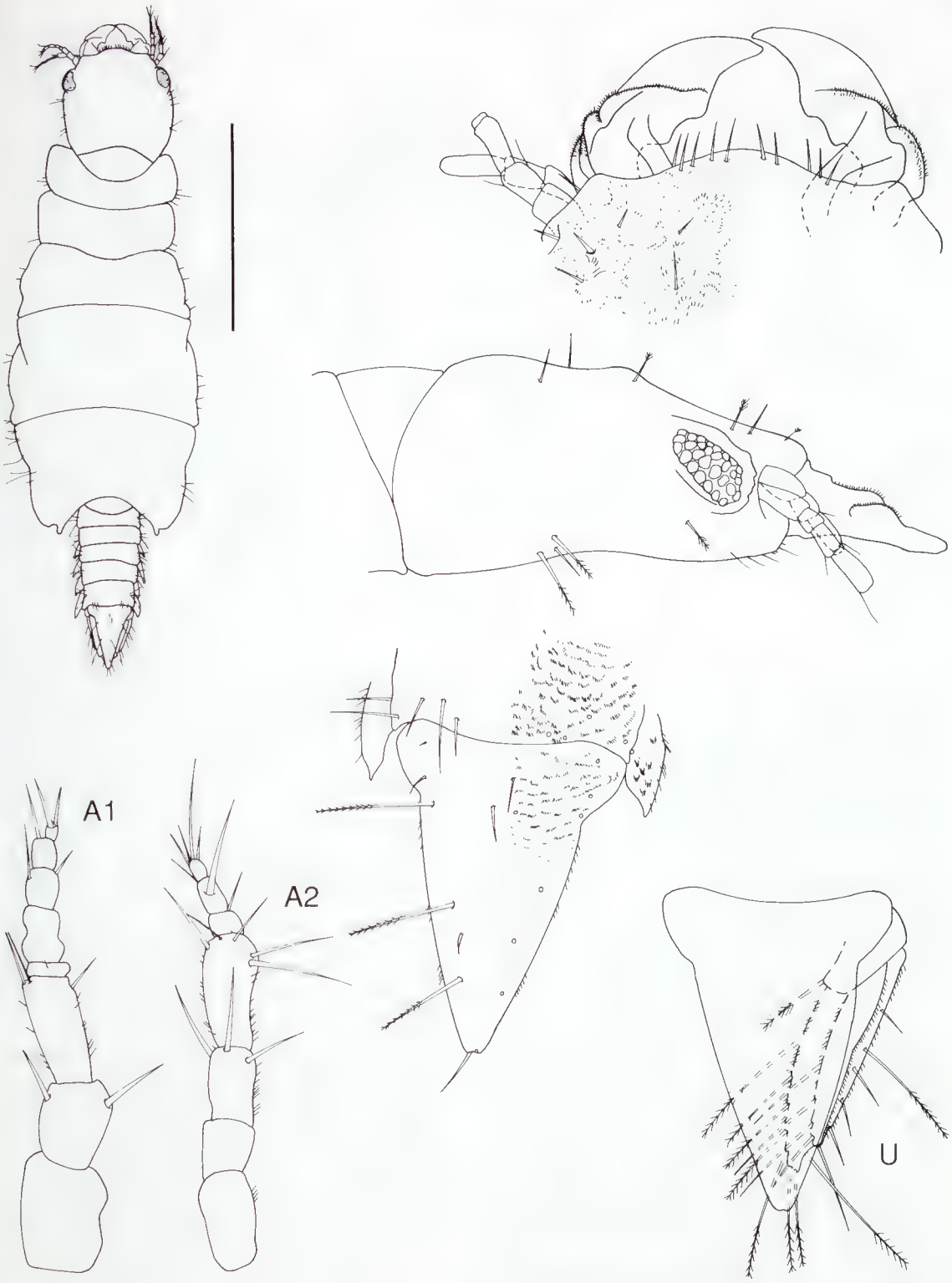


Figure 19. *Caecognathia branchyponera*. Holotype, NMV J27575.

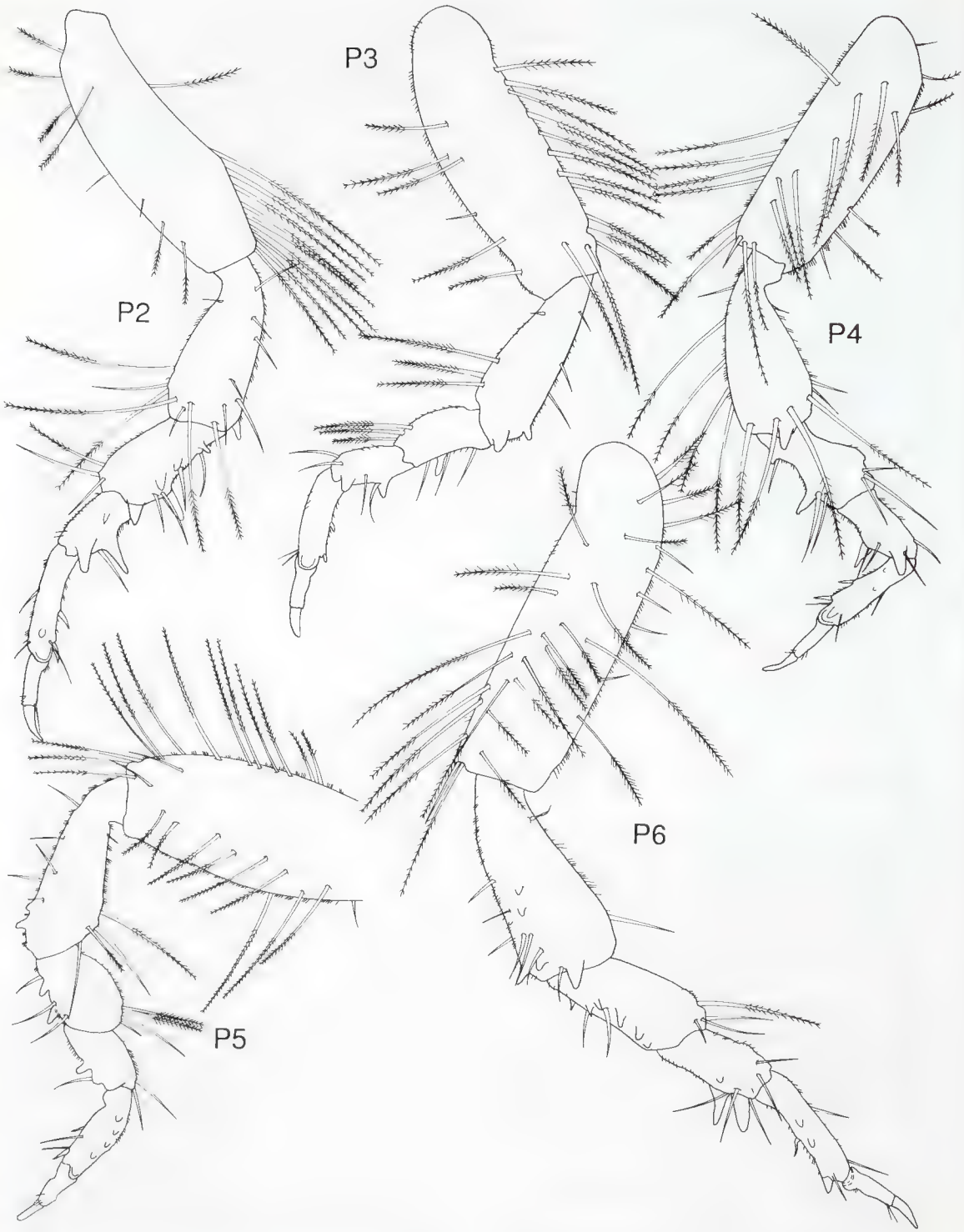


Figure 20. *Caecognathia branchyponera.* Holotype, NMV J27575.

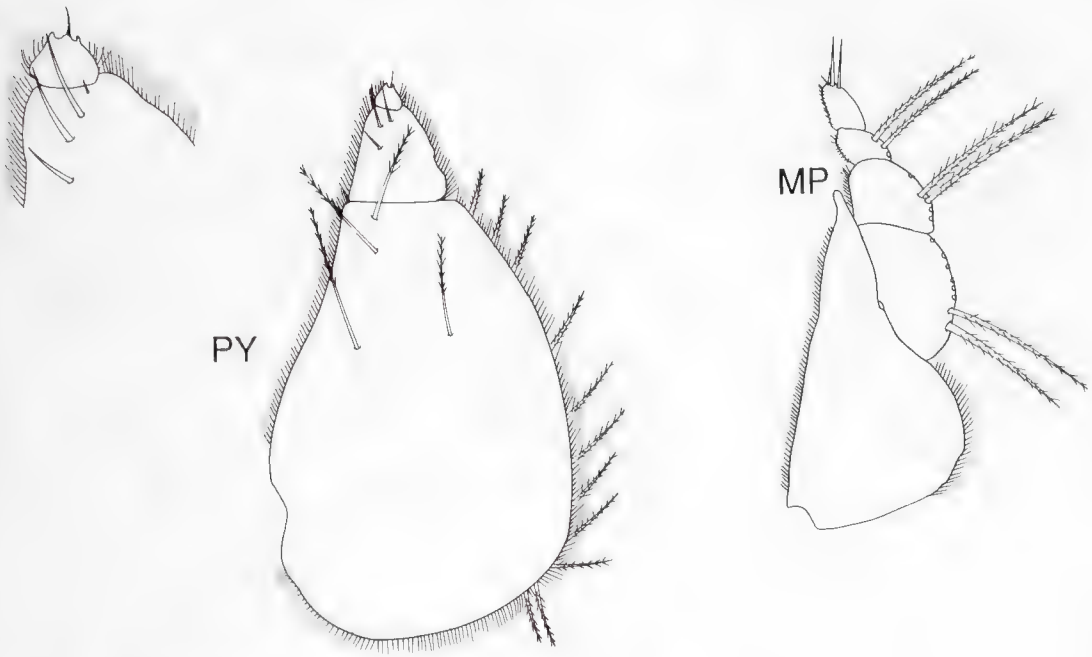


Figure 21. *Caecognathia branchyponera*. Holotype, NMV J27575.

143°22.1′E), 84 m, medium sand, WHOI epibenthic sled, M.F. Gomon et al. on RV *Hai Kung*, 31 Jan 1981 (stn BSS 120), NMV J27569 (1 male).

Paratypes. Tasmania, western Bass Strait, 59 km WNW of Cape Farewell, King I. (39°28′S, 143°17′E), 103 m, coarse sand, Smith-McIntyre grab, G.C.B. Poore on HMAS *Kimbla*, 10 Oct 1980 (stn BSS 81), NMV J8316 (3 males).

Victoria. Various collectors, 1980–1981. Western Bass Strait, 30 km SSW of Warrnambool (38°38.2′S, 142°35.0′E), 59 m, WHOI epibenthic sled (stn BSS 188), NMV J8321 (2 males). 51 km SSW of Cape Otway (39°16′S, 143°17′E), 90 m, medium sand, Smith-McIntyre grab (stn BSS 73), NMV J8320 (1 male). 35 km SSW of Cape Otway (39°06′S, 143°21′E), 59 m, coarse sand, Smith-McIntyre grab (stn BSS 57), NMV J8317 (2 males). 26 km SW of Cape Otway (39°01.0′S, 143°22.1′E), 84 m, medium sand, WHOI epibenthic sled (stn BSS 120), NMV J8313 (7 males). 25 km S of Cape Otway (39°06.7′S, 143°28.7′E), 92 m, fine sand, WHOI epibenthic sled (stn BSS 119), NMV J8312 (4 males). 11 km SSW of Cape Otway (38°58′S, 143°29′E), 67 m, medium sand, Smith-McIntyre grab (stn BSS 51), NMV J8319 (1 male). 15 km S of Cape Otway (39°00′S, 143°32′E), 79 m, medium sand (stn BSS 50, NMV J8318, (1 male). 25 km S of Cape Otway (39°06.0′S, 143°35.8′E), 95 m, fine sand, WHOI epibenthic sled (stn BSS 118), NMV J8315 (4 males), NMV J8314 (2 males).

*Description.* Total length of holotype: 5.29 mm.

Pale colour. Cephalosome elliptical; posterior margin only slightly curved, broad; cephalosome 1.3 times as long as wide, lateral margins convex. Eyes well developed, lateral and sessile. Frontal border slightly produced, rounded with slight median projection; 10 submaginal setae of differing sizes on each side of median projection. External scissura absent. Supraocular lobe smoothly convex. Antennae subequal; antenna 1 down-turned in lateral view, flagellum of 5 articles, long, only marginally shorter than peduncle, without aesthetascs; flagellum of antenna 2 of 6 articles. Mandible strongly curved, one-third length of cephalosome; with unarmed carina; smooth blade on distal two-thirds; basal neck smoothly arced; erisma pronounced. Maxilliped 5-articled, palp thin and elongate; external margins of articles 2–4 bearing plumose setae; endite clearly reaching article 3, wide. Pylopod 3-articled, with dense internal margin of plumose setae; article 1 with 75–80 plumose setae on ventral surface; article 2 conical, posterior margin completely joined to article 1, with 7 simple setae on ventral surface; article 3 minute.

Pereon width increasing posteriorly; widest at peronite 5, 1.5 times as wide as cephalosome, margins with numerous fine, short setae. Peronite 1 dorsally reaching lateral margins and

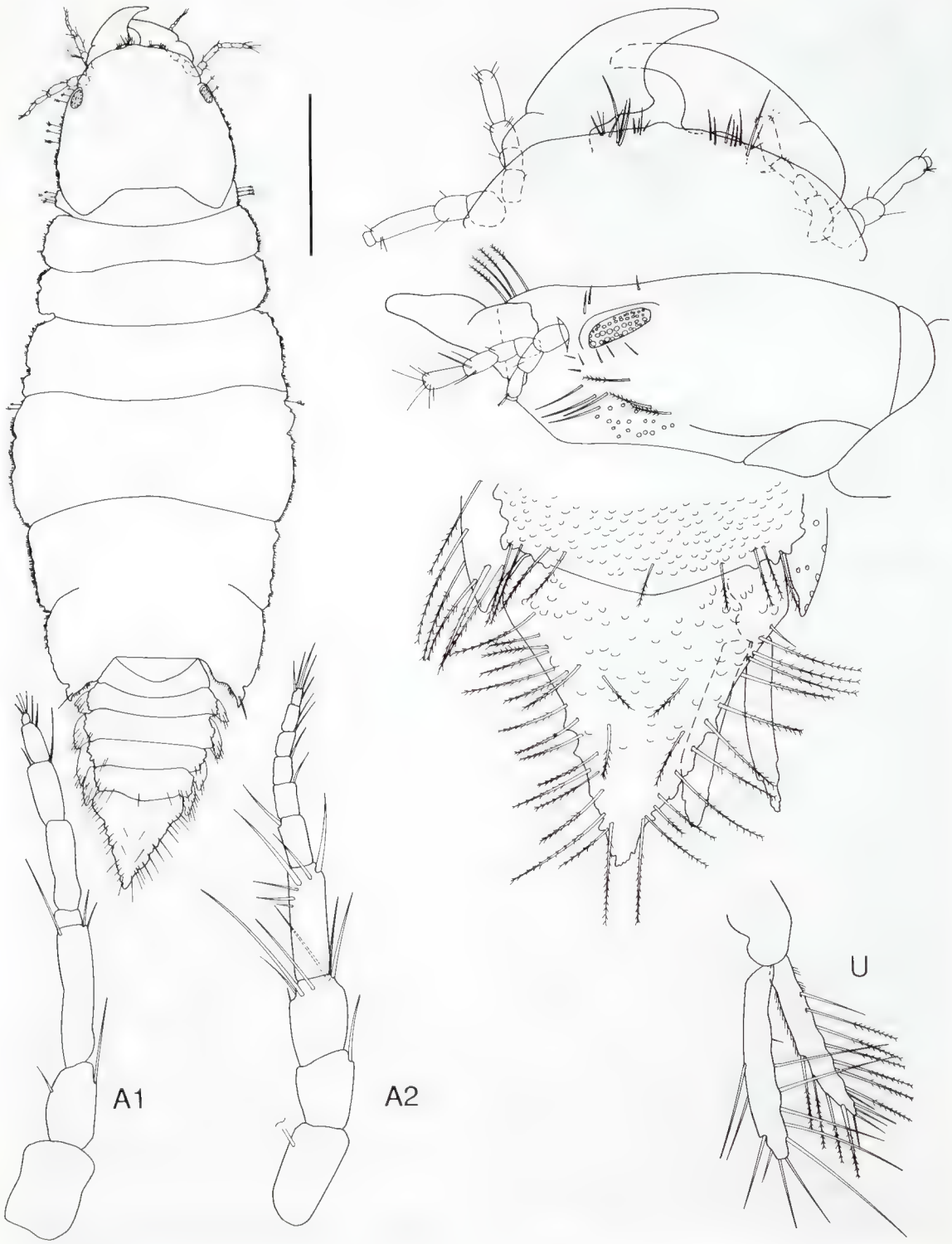


Figure 22. *Caecognathia diacamma*. Holotype, NMV J27569.

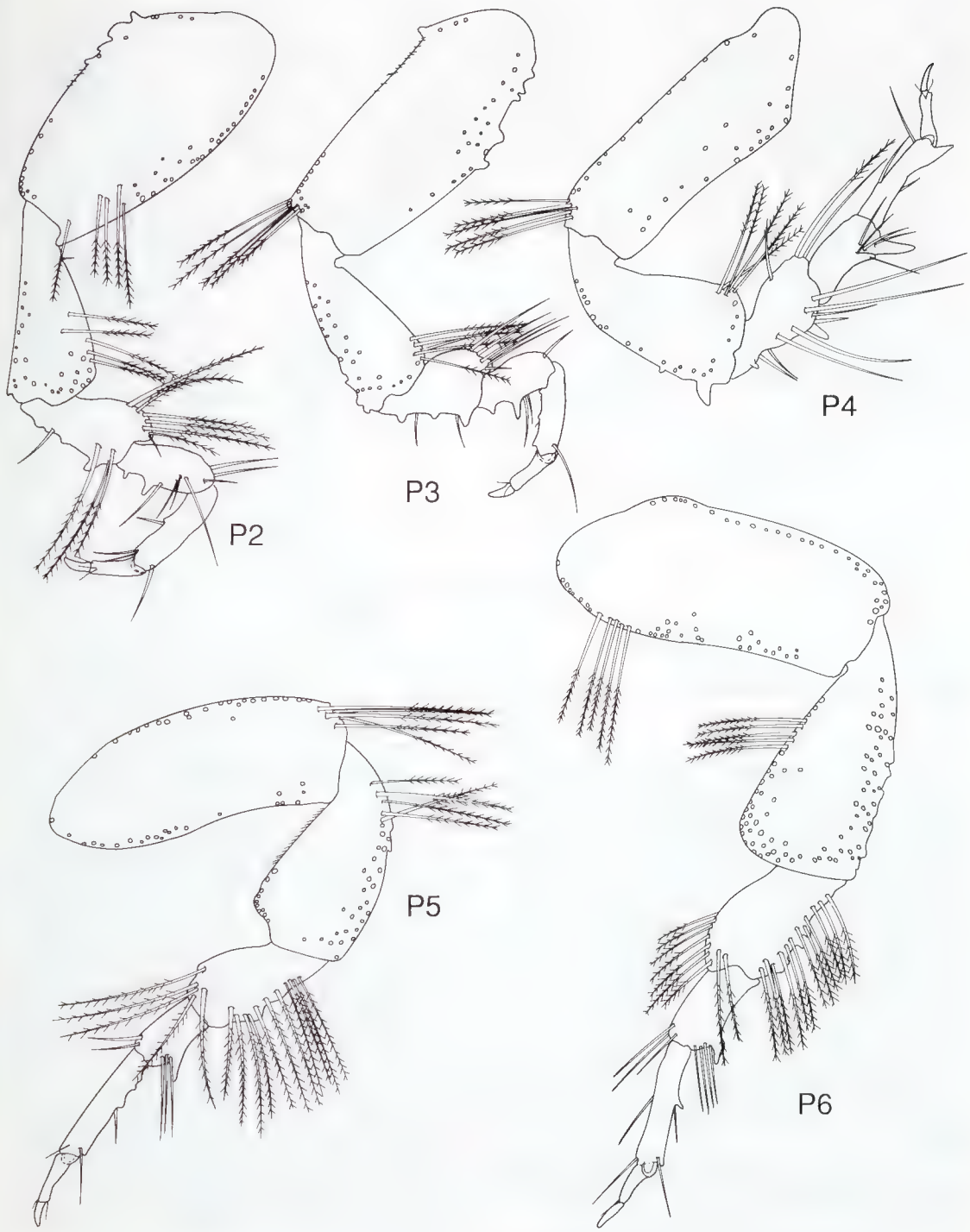


Figure 23. *Caecognathia diacamma*. Holotype, NMV J27569.

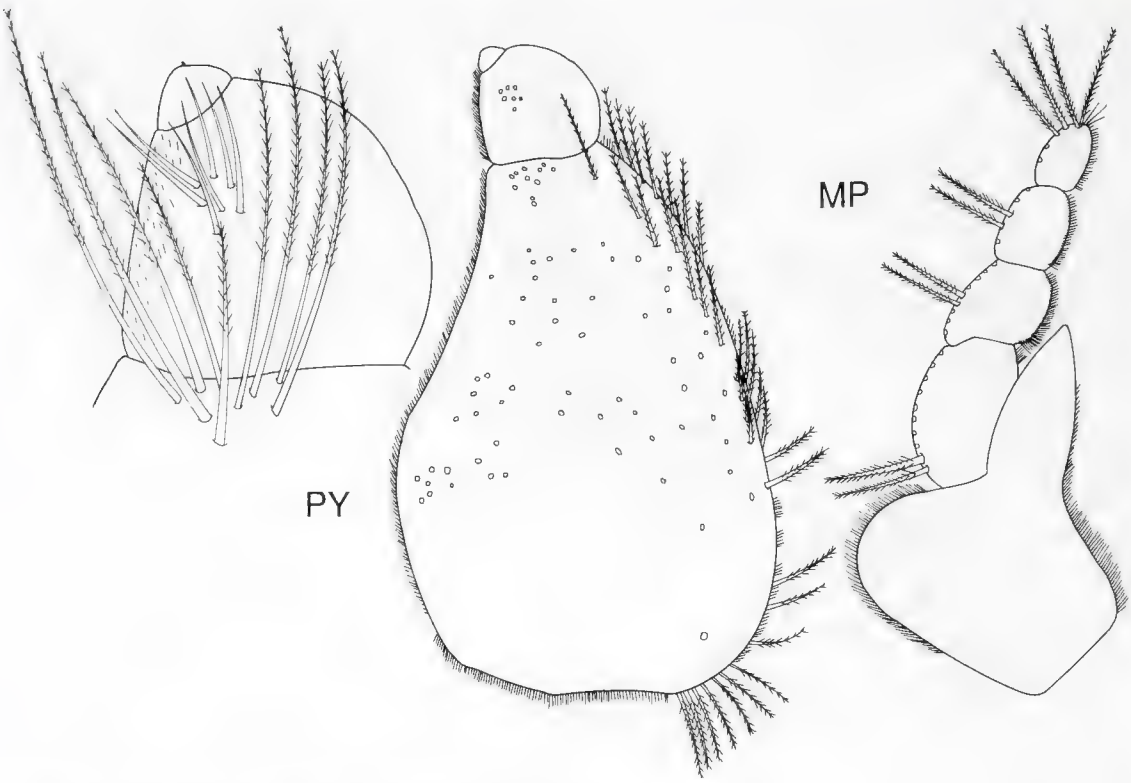


Figure 24. *Caecognathia diacamma*. Holotype, NMV J27569.

partially obscured laterally by pereonite 2. Pereonite 6 with pronounced globular lobuii and suture midway on lateral margins. Pereonite 7 very narrow, overlapping pleon. Pleon broad with irregular lateral borders; pleonites 1 and 5 narrower than others; epimera prominent. Pleotelson subtriangular, as wide as long, with numerous tubercules and 12–17 pairs of plumose setae laterally and 2 medianly. Uropod peduncle without setae; rami subequal, not reaching apex of pleotelson; exopod bearing numerous plumose setae.

Pereopods with dense cover of plumose setae; with few lateral projections on anterior faces of ischium to carpus; pereopod 4 smaller than others.

Pleopods setose. Pleopod 2 endopod lacking appendix masculina. Penes 2 small contiguous papillae.

*Distribution.* Western Bass Strait, 59–103 m.

*Remarks. Caecognathia diacamma* is characterised by the distinct suture on the lateral margins of pereonite 6.

### ***Caecognathia dolichoderus*** sp. nov.

Figures 25–27

*Material examined.* Holotype. Tasmania, eastern Bass Strait, 63 km E of North Point, Flinders I. (39°44.8′S, 148°40.6′E), 124 m, muddy sand, Smith-McIntyre grab, R.S. Wilson on RV *Tangaroa*, 14 Nov 1981 (stn BSS 167), NMV J27561 (1 male).

Paratypes. Most collected using WHOI epibenthic sled by R.S. Wilson on RV *Tangaroa*, Nov 1981. Tas. Eastern Bass Strait, 100 km NE of North Point, Flinders I. (38°52.6′S, 148°25.2′E), 130 m, fine sand (stn BSS 170), NMV J8333 (3 males). 85 km NE of North Point, Flinders I. (39°02.4′S, 148°30.6′E), 120 m, muddy sand (stn BSS 169), NMV J8335 (4 males). 60 km E of North Point, Flinders I. (39°41.7′S, 148°39.5′E), 115 m, muddy sand, naturalists' dredge, G.C.B. Poore on HMAS *Kimbla*, 27 Mar 1979 (stn BSS 32), NMV J8336 (2). 63 km E of North Point, Flinders I. (39°44.8′S, 148°40.6′E), 124 m, muddy sand, Smith-McIntyre grab (stn BSS 167), NMV J8334 (1 male).

*Description.* Total length of holotype: 3.15 mm.

Cephalosome rectangular with pronounced

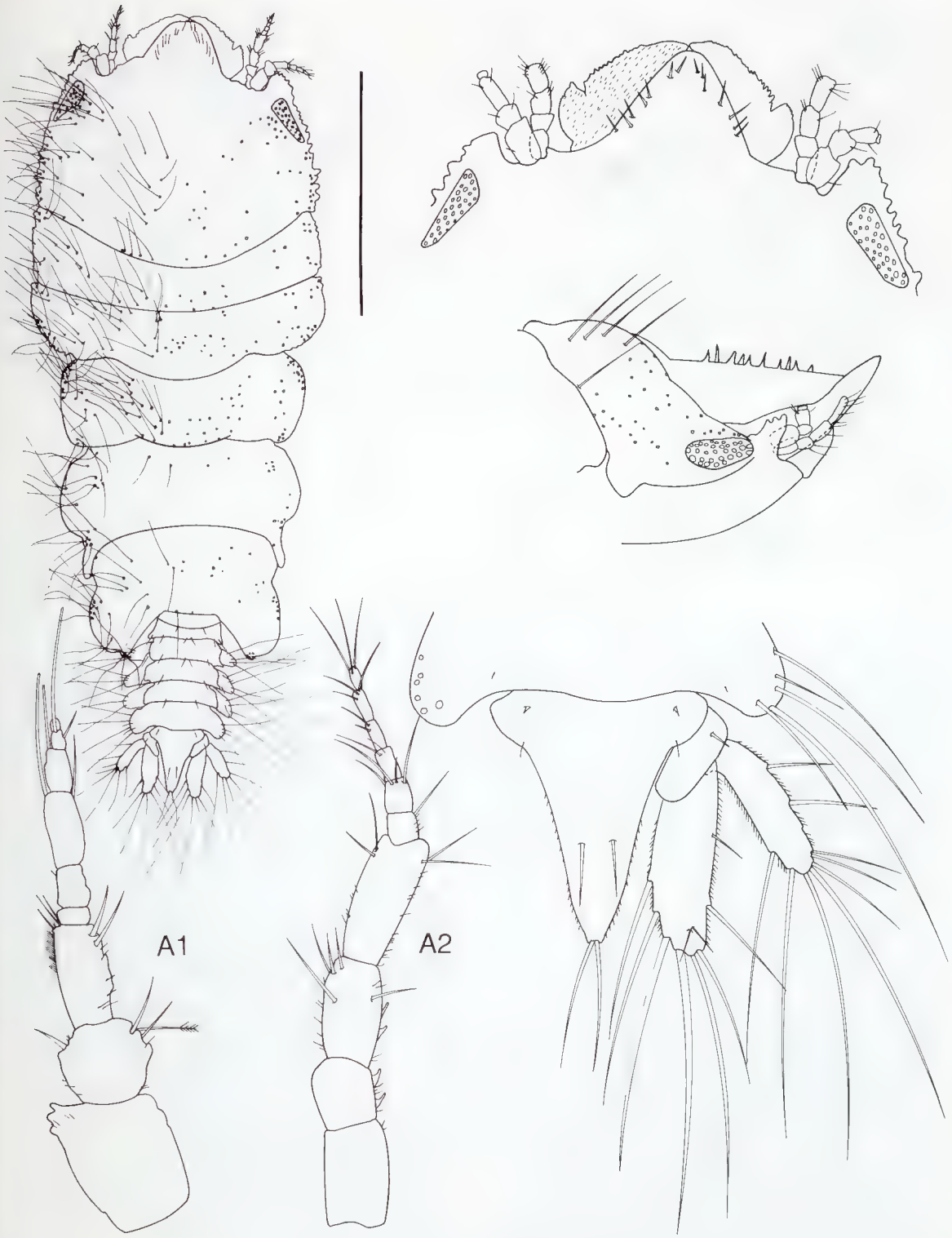


Figure 25. *Caecognathia dolichoderus*. Holotype, NMV J27561.

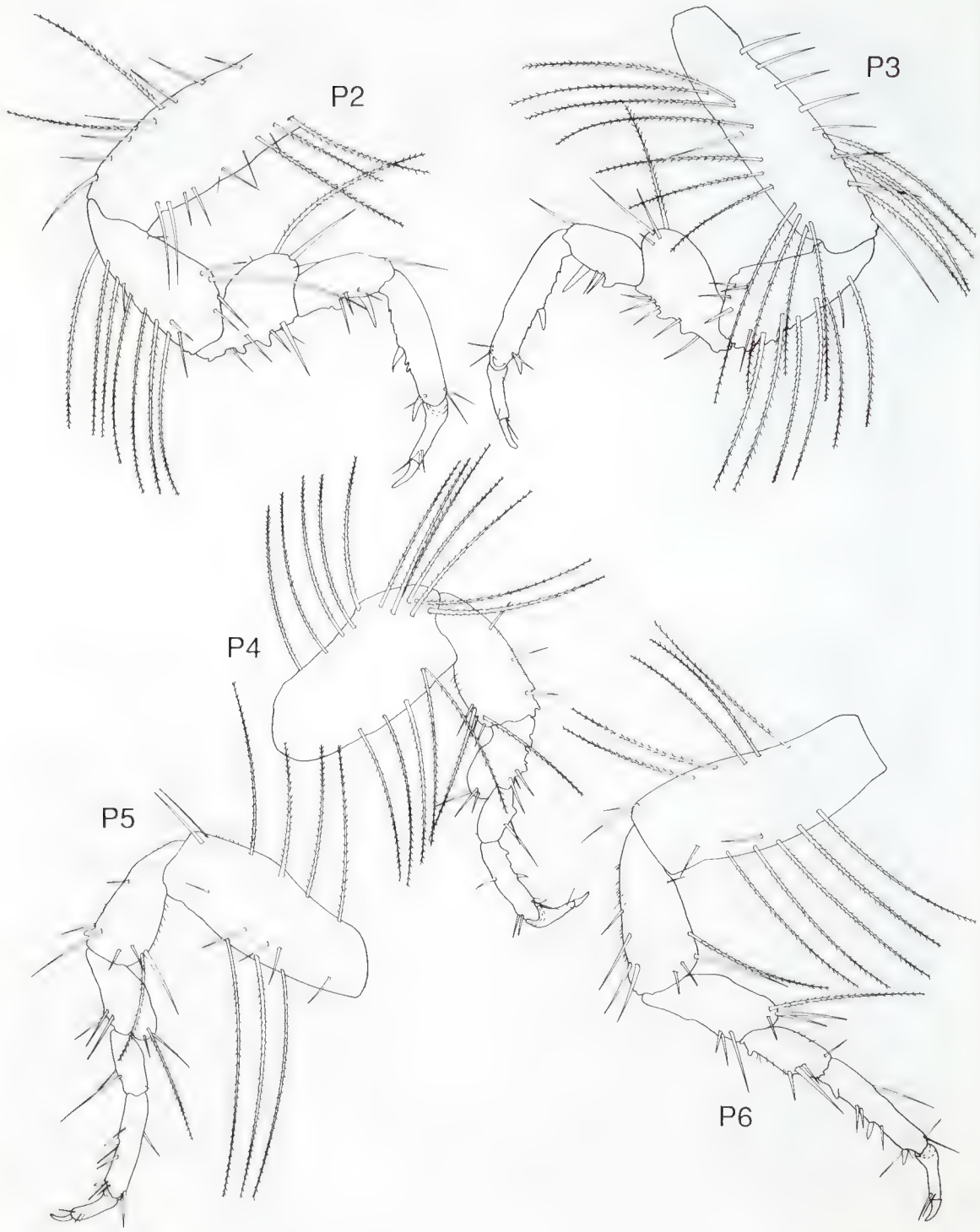


Figure 26. *Caecognathia dolichoderus*. Holotype, NMV J27561.

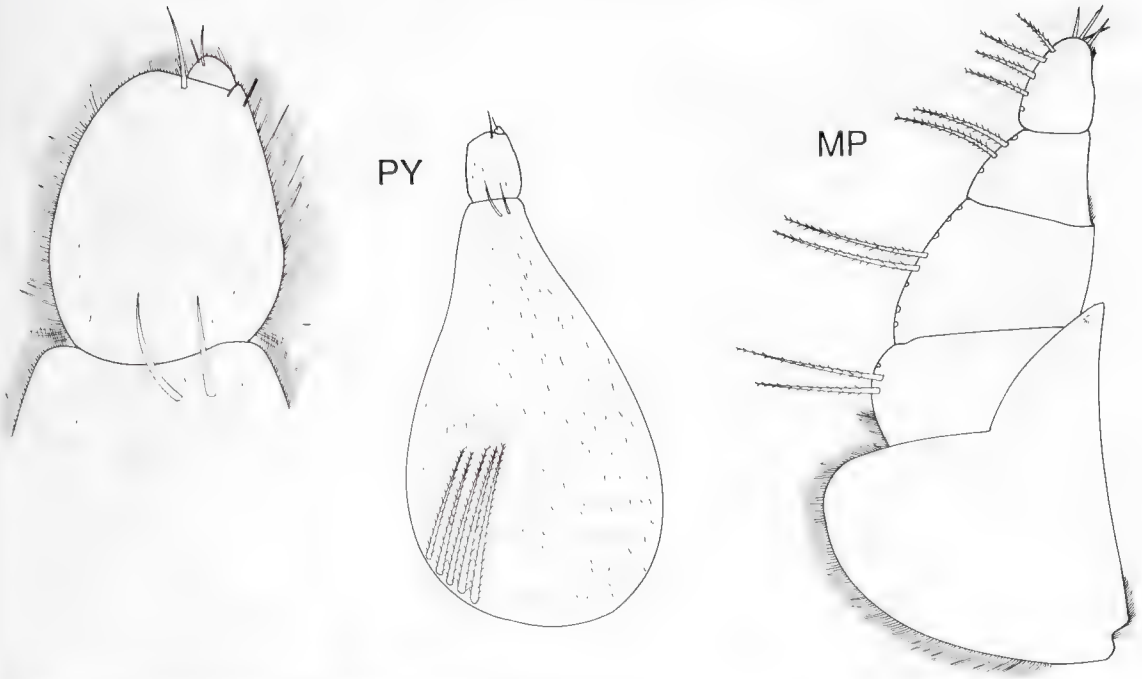


Figure 27. *Caecognathia dolichoderus*. Holotype, NMV J27561.

rostrum, 1.15 times as wide as long, lateral margins convex and irregular. Eyes well developed, lateral and sessile. Frontal border produced as rostrum, smoothly rounded with 14 setae spread submarginally. External scissura rounded. Supraocular lobe not pronounced. Cephalosome with many small spines anteriorly, visible in lateral view. Antennae stout, subequal; flagellum of antenna 1 of 5 articles, with 3 aesthetascs; flagellum of antenna 2 of 6 articles. Mandible one-third length of cephalosome with sparse covering of small fine setae; armed carina; pronounced mandibular incisor; mandible tightly closing around rostrum. Maxilliped 5-articled; external margins of articles 2–4 bearing plumose setae; endite clearly reaching article 3, wide, with 1 coupling hook. Pylopod 3-articled, internal margin lacking long setae; article 1 with 2 setae on ventral surface distally and 5 plumose setae at basis; article 2 with 1 seta on ventral surface; article 3 minute.

Pereon dorsoventrally flattened; widest anteriorly, as wide as cephalosome; covered with numerous long simple setae. Pereonite 1 dorsally fused with cephalosome and not visible laterally. Pereonites 2 and 3 subequal, pereonites 4–6 narrower and longer than 2 and 3; pereonite 6 with small, rounded lobuii. Pereonite 7 very narrow, overlapping pleon. Pleonites progressively longer and wider, epimera prominent. Pleotelson subtriangular, longer than wide; lateral margins straight; with 2 pairs of simple setae and pair of setae on distal apex. Uropodal peduncle with 1 seta; endopod longer than exopod, reaching apex of pleotelson margins; rami bearing long simple setae.

Pereopods with moderate cover of large plumose setae, particularly on basis and ischium; elsewhere few, short simple setae. Pereopods 2 and 3 with few acute projections on lateral faces of merus–carpus.

Pleopods setose. Pleopod 2 endopod lacking appendix masculina. Penes 2 small contiguous papillae.

*Distribution.* Eastern Bass Strait, 115–130 m.

*Remarks. Caecognathia dolichoderus* does not closely resemble any previously described species. It is characterised by flat mandibles with a large incisor and very well armed carina, which fit snugly around the rostrum.

### ***Caecognathia gnamptogenys*** sp. nov.

Figures 28–30

*Material examined.* Holotype. Victoria, S of Point Hicks (38°21.90′S, 149°20.00′E), 1000 m, WHOI epibenthic sled, G.C.B. Poore et al. on RV *Franklin*, 23 Jul 1986 (stn SLOPE 32), NMV J19116 (1 male).

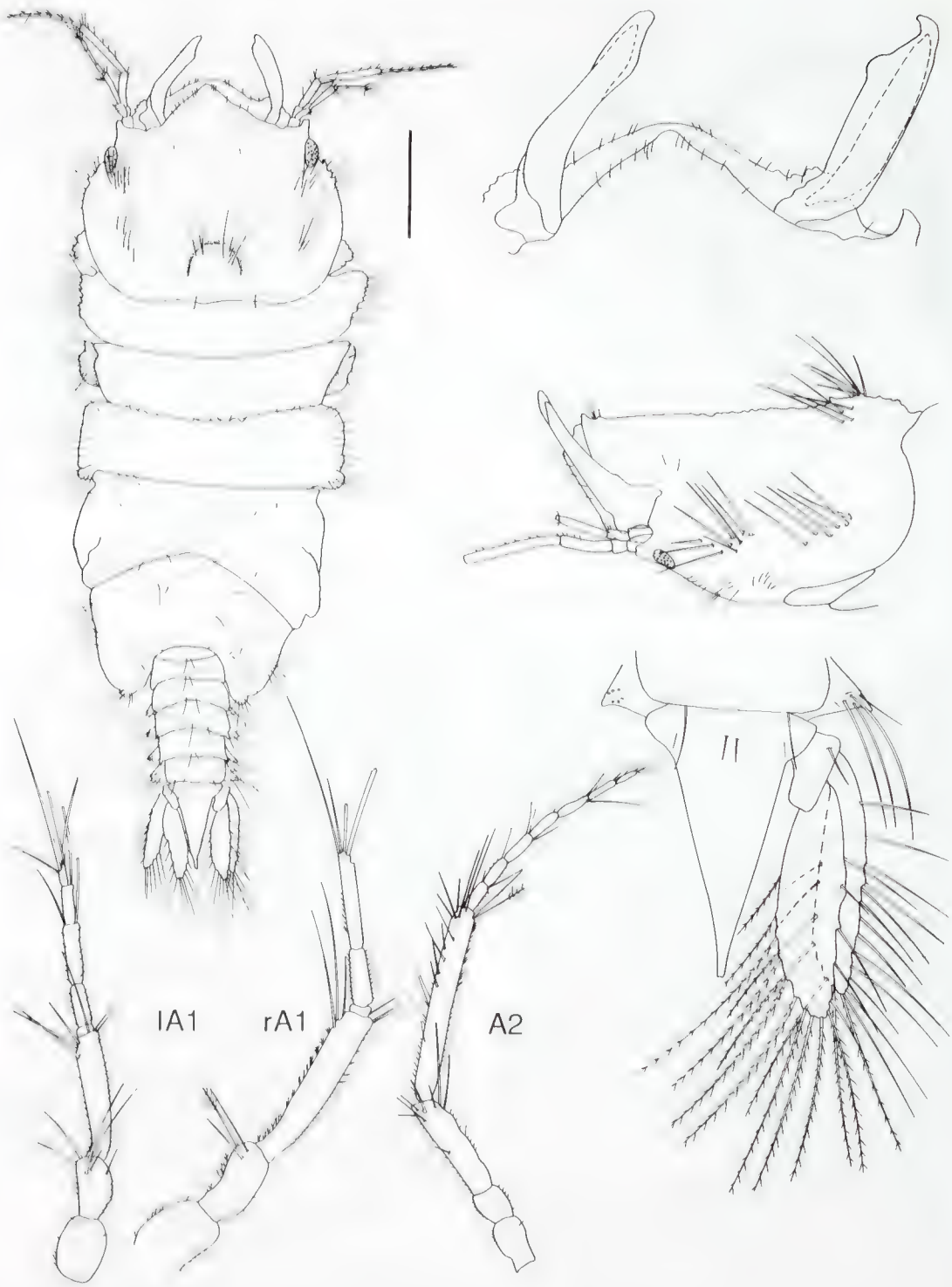


Figure 28. *Caecognathia gnamptogenys*. Holotype, NMV J19116.

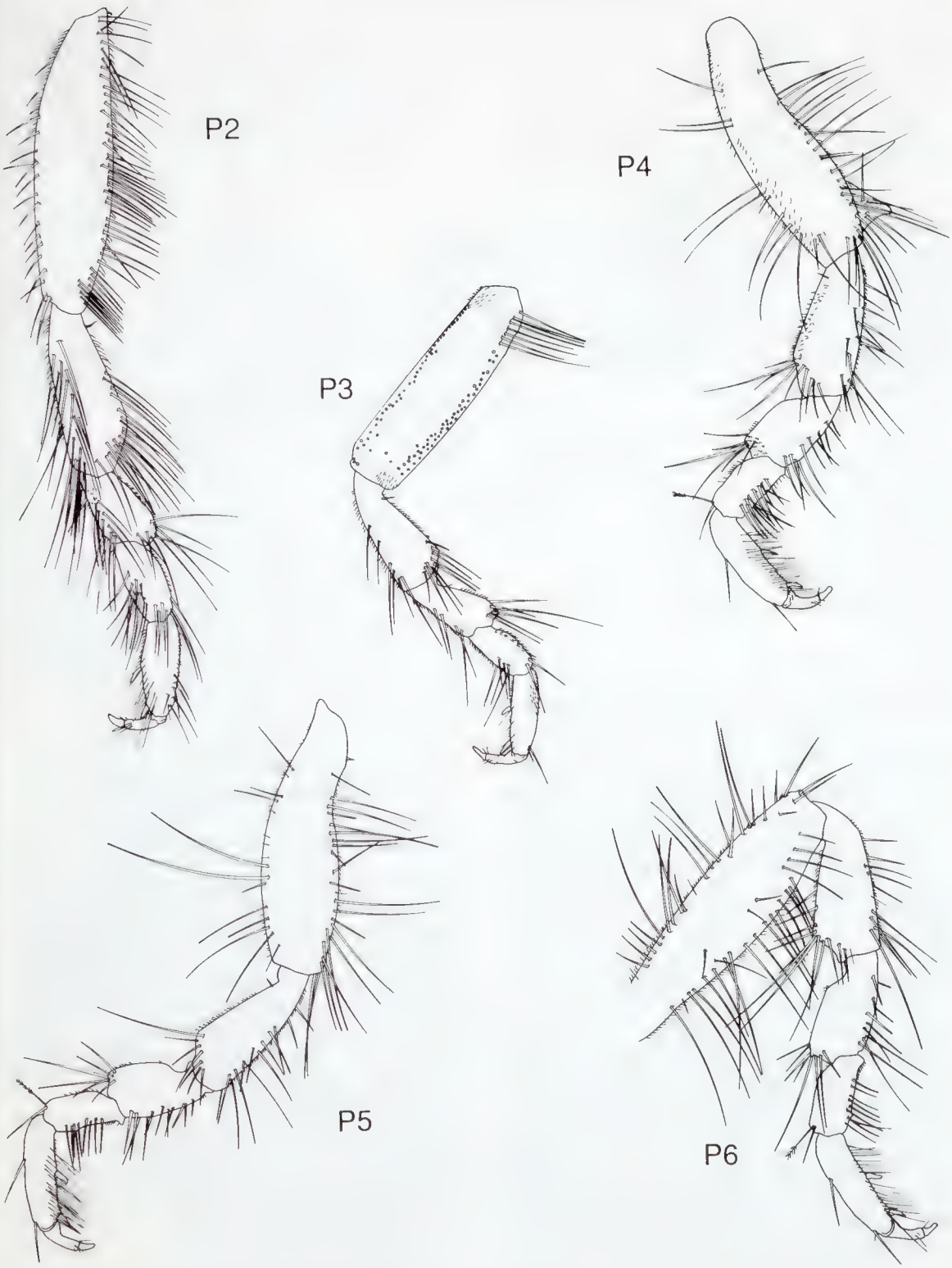


Figure 29. *Caecognathia gnamptogenys*. Holotype, NMV J19116.

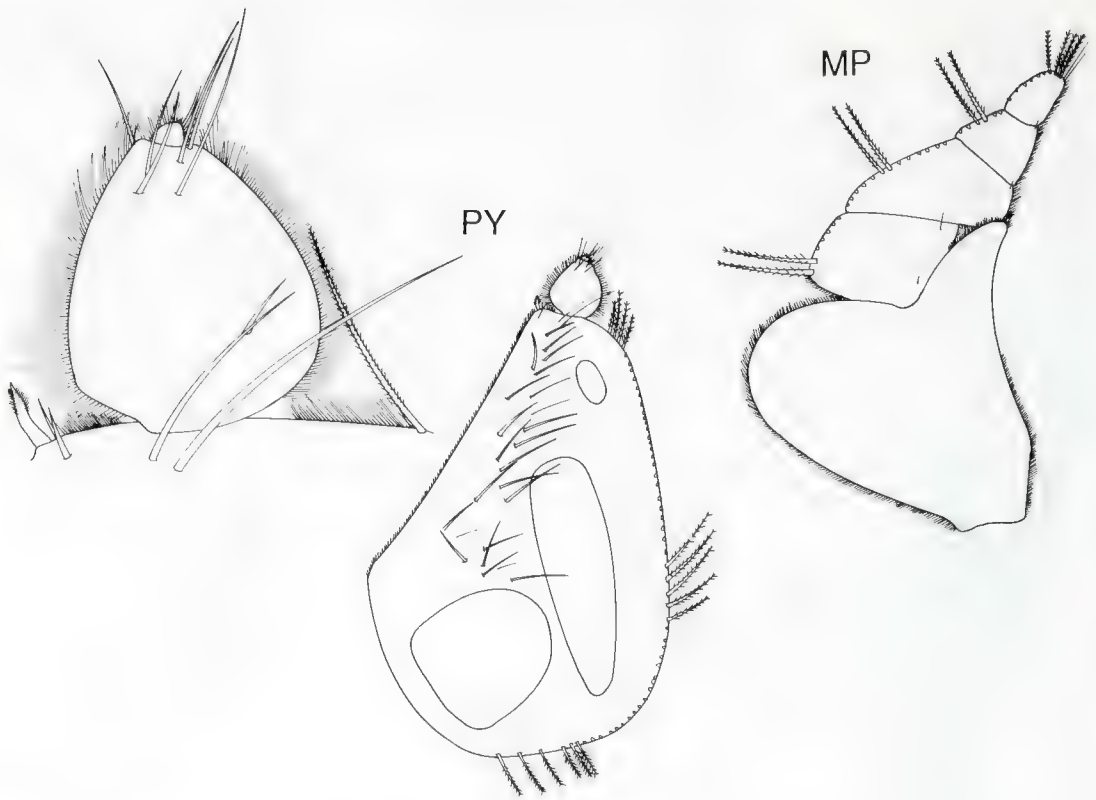


Figure 30. *Caecognathia gnamptogenys*. Holotype, NMV J19116.

*Description*. Total length of holotype: 7.4 mm.

Cephalosome quasipentagonal, lateral margins posterior to eyes rounded, frontal margin rounded. Eyes ventrolateral. Frontal border produced, conical, with 12 setae submarginally each side in 2 rows of 6: 1 row on rounded ventral buccal wall extension; other row on frontal border. Lamina dentata visible. External scissura very shallow. Supraocular lobe very low, acute. Cephalosome with low, posterior median tubercle with 6–7 long setae. Antenna 2 longer than antenna 1; flagellum of antenna 1 of 5 articles, with 3 aesthetascs; flagellum of antenna 2 of 7 articles (right antenna 1 flagellum of only 3 articles and 1 aesthetasc, terminal article as long as 3 and 4 articles of left flagellum). Mandible straight, raised in lateral view, one-third length of cephalosome; cylindrical, lacking obvious blade; with unarmed carina. Maxilliped 5-articled; external margins of articles 2–4 bearing plumose setae; endite barely reaching article 3. Pylopod 3-articled, with internal margin of plumose setae; article 1 with 3 areolae, second areola very elongate, with 27 setae on ventral surface medianly; article 2 with 7 setae on ventral surface distally; article 3 minute.

Pereon widest anteriorly, wider than cephalosome, covered with numerous simple setae. Pereonite 1 dorsally fused with cephalosome, visible as 2 small regions laterally on cephalosome. Pereonite 3 with ventrolateral extensions, pereonites 5 and 6 together as long as 2 to 4 together. Pereonite 7 very narrow, overlapping pleon. Pleonites subequal, pleonal epimera prominent. Pleotelson elongate, 1.5 times as long as wide, with 2 pairs of simple setae. Uropodal peduncle with 1 seta; rami subequal, reaching apex of pleotelson; internal margins of rami bearing numerous plumose setae.

Pereopods with dense cover of simple setae. Pereopod 3 smaller than others; basis of pereopod 4 with distal conical projection.

Pleopods setose. Pleopod 2 endopod with appendix masculina half length of rami. Penes 2 small contiguous papillae.

*Distribution*. Eastern slope of Bass Strait, 1000 m.

*Remarks.* *Caecognathia gnamptogenys* is characterised by the distal expansion of the basis of pereopod 4; eyes situated more ventrolaterally than in other species; and short and simple mandibles. *C. serrata* (Richardson) from the Atlantic Ocean shares similar features but possesses a greatly produced frontal border.

### ***Caecognathia huberia*** sp. nov.

Figures 31–33

*Material examined.* Holotype. Victoria, western Bass Strait, 50 km SSW of Warrnambool (38°49.5′S, 142°35.4′E), 89 m, coarse sand, R.S. Wilson on RV *Tangaroa*, 21 Nov 1981 (stn BSS 190), NMV J27565 (1 male).

Paratypes. Tasmania, western Bass Strait, 59 km W of Stokes Point, King I. (40°07′S, 143°14′E), 185 m, sandy mud, Smith-McIntyre grab, G.C.B. Poore on HMAS *Kimbla*, 11 Oct 1980 (stn BSS 104), NMV J8364 (1 male).

Victoria, western Bass Strait, 50 km SSW of Warrnambool (38°49.5′S, 142°35.4′E), 89 m, coarse sand, R.S. Wilson on RV *Tangaroa*, 21 Nov 1981 (stn BSS 190). NMV J8363 (3 males). 5 km S of Point Reginald (38°48.0′S, 143°14.5′E), 47 m, hard rocky bottom, R.S. Wilson on RV *Tangaroa*, 20 Nov 1981 (stn BSS 185), NMV J8362 (2 males). Eastern Bass Strait, 11.7 km W of Pt Ricardo (37°49.89′S, 148°30.13′E), 27 m, coarse sand, Smith-McIntyre grab, N. Coleman on RV *Sarda* (stn MSL-EG 105), NMV J24635 (3 males); (stn MSL-EG 78) NMV J24634 (1 male). 7.3 km SSW of Cape Conran (37°52.65′S, 148°42.15′E), 49 m, coarse sand, Smith-McIntyre grab, N. Coleman on RV *Sarda*, Feb 1991 (stn MSL-EG 116), NMV J24636 (1 male).

*Description.* Total length of holotype: 2.99 mm.

Eyes well developed, lateral and sessile. Frontal border produced medianly, truncated, with 2 slight lateral depressions near internal margin of mandible; 6 short setae medianly and 4 longer setae laterally. External scissura deep, smoothly rounded. Supraocular lobe not pronounced. Cephalosome and pereon with numerous granules and long simple setae; with anterior, mesial furrow and shallower, oblique posterior mesolateral furrows and low, posterior median tubercle. Antennae stout, down-turned; antenna 1 longer than antenna 2, flagellum of 4 articles, with 3 aesthetascs; flagellum of antenna 2 of 4 articles, shorter than article 4 of peduncle. Mandible curved inward, one-third length of cephalosome, slightly asymmetrical; with unarmed carina; pronounced mandibular incisor one-third to half way along; short setae near incisor; smooth arc-shaped blade on distal half with long irregular basal neck proximally giving blade produced and irregular appearance. Maxilliped 5-articled; external margins of articles 2–4 bearing plumose setae; endite barely reaching article 3, with 2 coupling hooks. Pylopod 2-articled, article 2 small; internal margin of fine short setae; article 1 operculate, with 4 setae distally on ventral surface; article 2 with 6 setae on ventral surface.

Pereon evenly sided, as wide as cephalosome. Pereonite 1 barely reaching lateral margins dorsally and partially obscured laterally by pereonite 2. Pereonites progressively longer. Pereonite 4 with slight anterior constriction; small, anteriorly directed median spine and smoothly rounded median extension of posterior margin. Pereonite 5 with dorsal sulcus and areae laterales. Pereonite 6 with lobi laterales and rounded lobuii. Pereonite 7 very narrow, overlapping pleon. Pleon progressively narrower, with numerous large setae; pleonal epimera prominent. Pleotelson subtriangular, wider than long, with pair of simple setae medianly and pair of setae on distal apex. Uropodal peduncle with 1 seta; endopod longer than exopod, reaching beyond the apex of pleotelson; rami margins with a few long simple setae.

Pereopods subequal, with few simple setae; few lateral projections, mainly on carpus and merus; tubercles on basis of pereopod 3 and basis-merus of pereopod 6.

Pleopods without setae. Pleopod 2 endopod lacking appendix masculina. Penes 2 small contiguous papillae.

*Distribution.* Bass Strait, 27–185 m.

*Remarks.* *Caecognathia huberia* belongs to a complex of south-eastern Australian species most easily recognised by the mesial and oblique posterior grooves on the cephalon. The other species in this complex are *C. pustulosa* (Hale), *C. agwillisi* (Seed) and *C. paratrechia*. *C. huberia* is very similar to *C. pustulosa* (Hale) but differs by being hirsute, particularly anteriorly; possessing a smaller anterior spine on pereonite 4; possessing a distinct posterior extension on peronite 4; smoothly rounded external scissura; and mandibles with a more complex blade and pronounced incisors.

### ***Caecognathia leptanilla*** sp. nov.

Figures 34–36

*Material examined.* Holotype. Tasmania, central Bass Strait, 25 km SW of Cape Frankland, Flinders I., (40°09.4′S, 147°32.6′E), 51 m, shelly sand, WHOI epi-

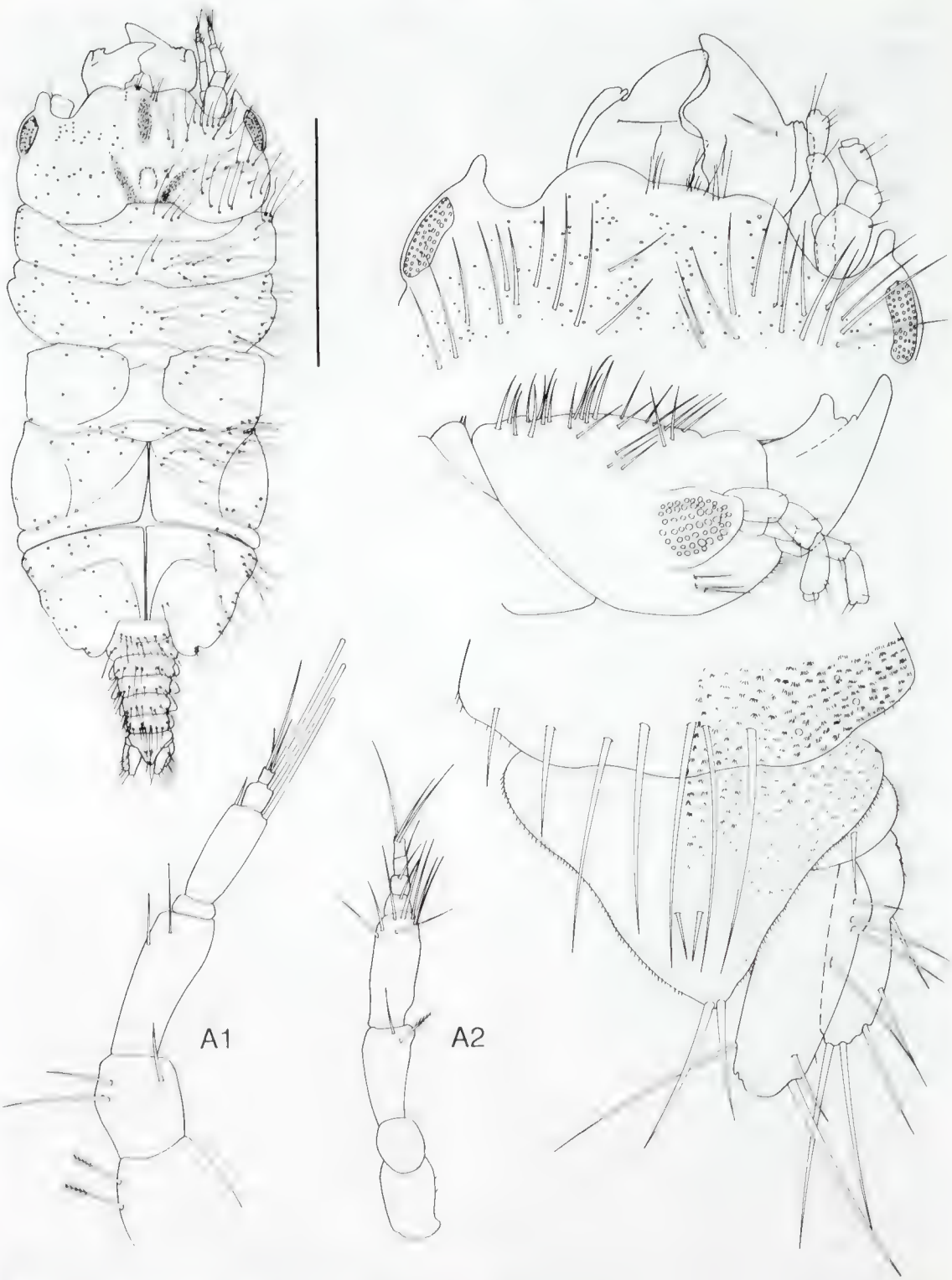


Figure 31. *Caecognathia huberia*. Holotype, NMV J27565.

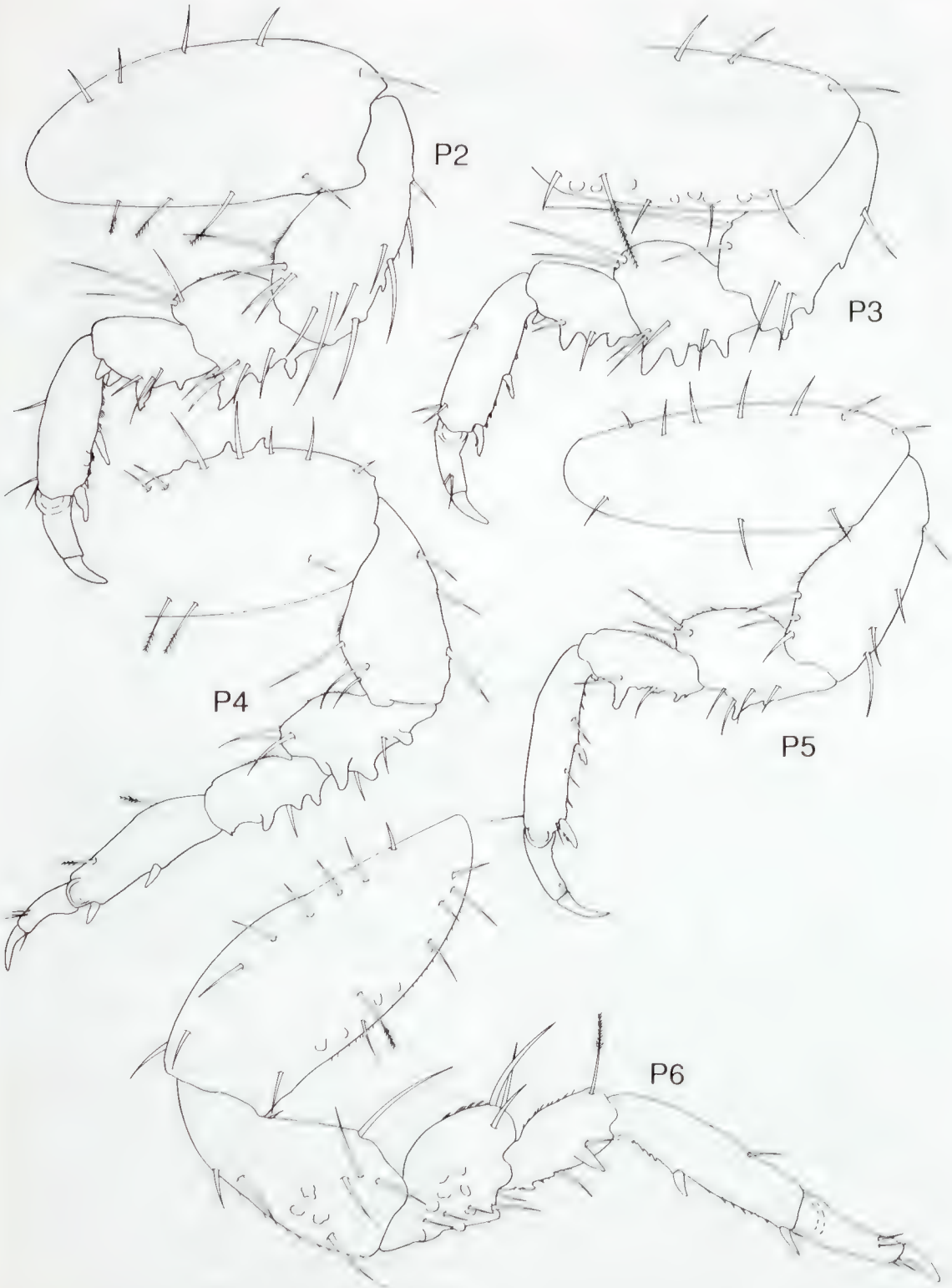


Figure 32. *Caecognathia huberia*. Holotype, NMV J27565.

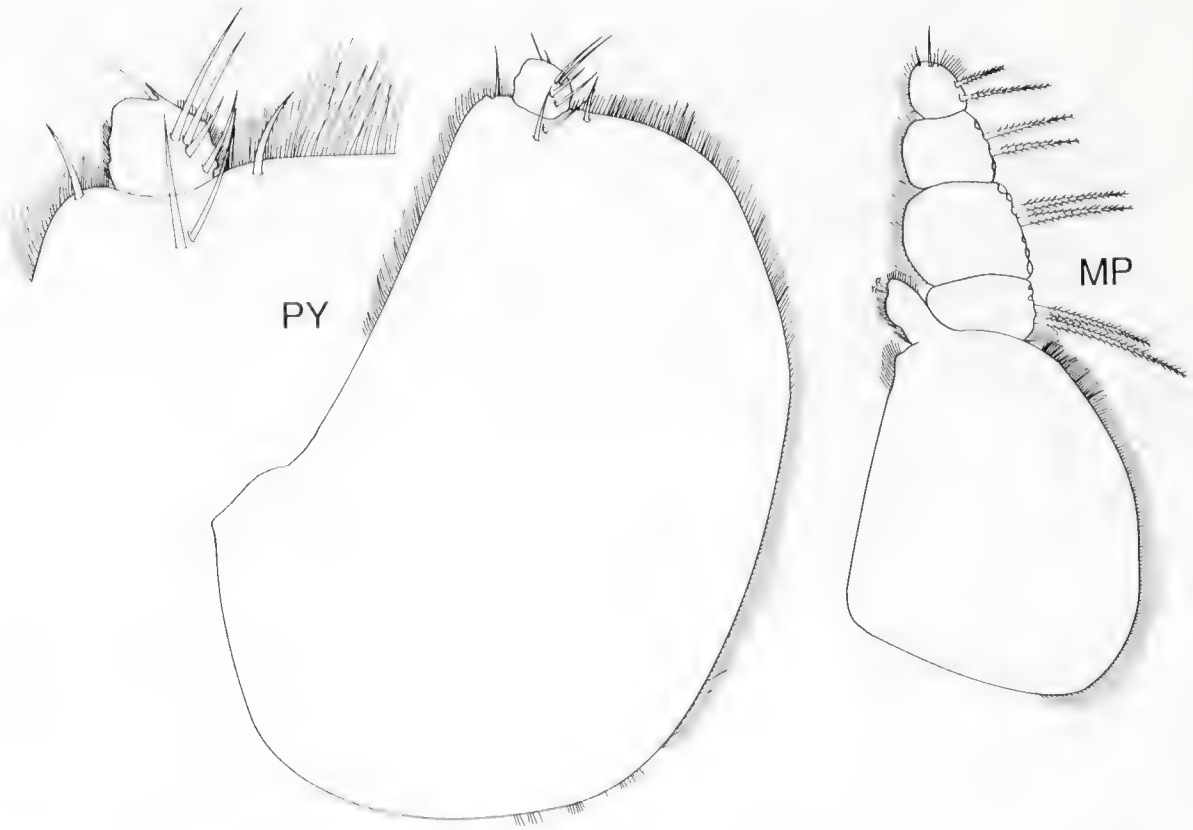


Figure 33. *Caecognathia huberia*. Holotype, NMV J27565.

benthic sled, R.S. Wilson on RV *Tangaroa*, 14 Nov 1981 (stn BSS 162), NMV J27562 (1 male).

Paratypes. Most collected by R.S. Wilson on RV *Tangaroa* using WHOI epibenthic sled, Nov 1981. Tasmania, western Bass Strait, 70 km W of Cape Farewell, King I., (39°38.2′S, 143°07.2′E), 127 m, mainly sand (stn BSS 195) NMV J8340 (1 male). Central Bass Strait, 44 km NE of Cape Wickham, King I. (39°22.0′S, 144°18.3′E), 60 m, coarse sand (stn BSS 203), NMV J8348 (1 male). 33 km S of Deal I. (39°48.3′S, 147°19.2′E), 60 m, muddy sand, Smith-McIntyre grab (stn BSS 161) NMV J8347 (1 male). 25 km SW of Cape Frankland, Flinders I. (40°09.4′S, 147°32.6′E), 51 m, shelly sand (stn BSS 162), NMV J8339 (4 males). Eastern Bass Strait, 20 km SSW of Babel I. (40°06.8′S, 148°24.3′E), 22 m, coarse shell, Smith-McIntyre grab (stn BSS 166), NMV J8344 (3 males). 37 km NNE of Eddystone Point (40°40.7′S, 148°36.9′E), 67 m, muddy sand (stn BSS 164), NMV J8338 (1 male).

Victoria. Western Bass Strait, 80 km WSW of Cape Otway (39°59′S, 142°37′E), 94 m, coarse sand, G.C.B. Poore on HMAS *Kimbla*, 9 Oct 1980 (stn BSS 62), NMV J8343 (1 male). 57 km SSW of Cape Otway (39°17′S, 143°14′E), 90 m, coarse carbonate sand, G.C.B. Poore on HMAS *Kimbla*, 10 Oct 1980 (stn BSS 72) NMV J8349 (1 male). Central Bass Strait, 6 km S of Cape Schanck (38°33.4′S, 144°54.9′E), 55 m, medium sand (stn BSS 154), NMV J8560 (1 male). 38 km SW of Cape Paterson (38°56.4′S, 145°16.6′E), 70 m, fine sand (stn BSS 155), NMV J8341 (4 males), J35492 (1 male). Eastern Bass Strait, 8 km S of Wilsons Promontory (39°12.9′S, 146°27.3′E), 65 m, medium sand (stn BSS 180), NMV J8345 (1 male). 43 km SE of Port Albert (38°53.7′S, 147°06.5′E), 58 m, coarse shell (stn BSS 177), NMV J8342 (2 males). 50 km SE of Port Albert (38°54.3′S, 147°13.4′E), 58 m, coarse shell, Smith-McIntyre grab (stn BSS 176), NMV J8346 (1 male).

Other material. 27 lots from 27–800 m depth in eastern Bass Strait and Tasmania, NMV collections.

*Description*. Total length of holotype: 5.08 mm.

Cephalosome roughly elliptical, 1.3 times as long as wide, lateral margins slightly convex. Eyes well developed, lateral and sessile. Frontal border produced dorsally into rostrum; smoothly rounded, with 10 submarginal setae of uniform size each side of mid-dorsal line. External scissura absent. Supraocular lobe smoothly convex. Antennae subequal, downturned in lateral view; flagellum of antenna 1 of 5 articles, with 3 aesthetascs; flagellum of antenna 2 of 6 articles. Mandible strongly curved, one-third length of cephalosome; with unarmed carina; smooth blade. Maxilliped 5-articled, palp thin

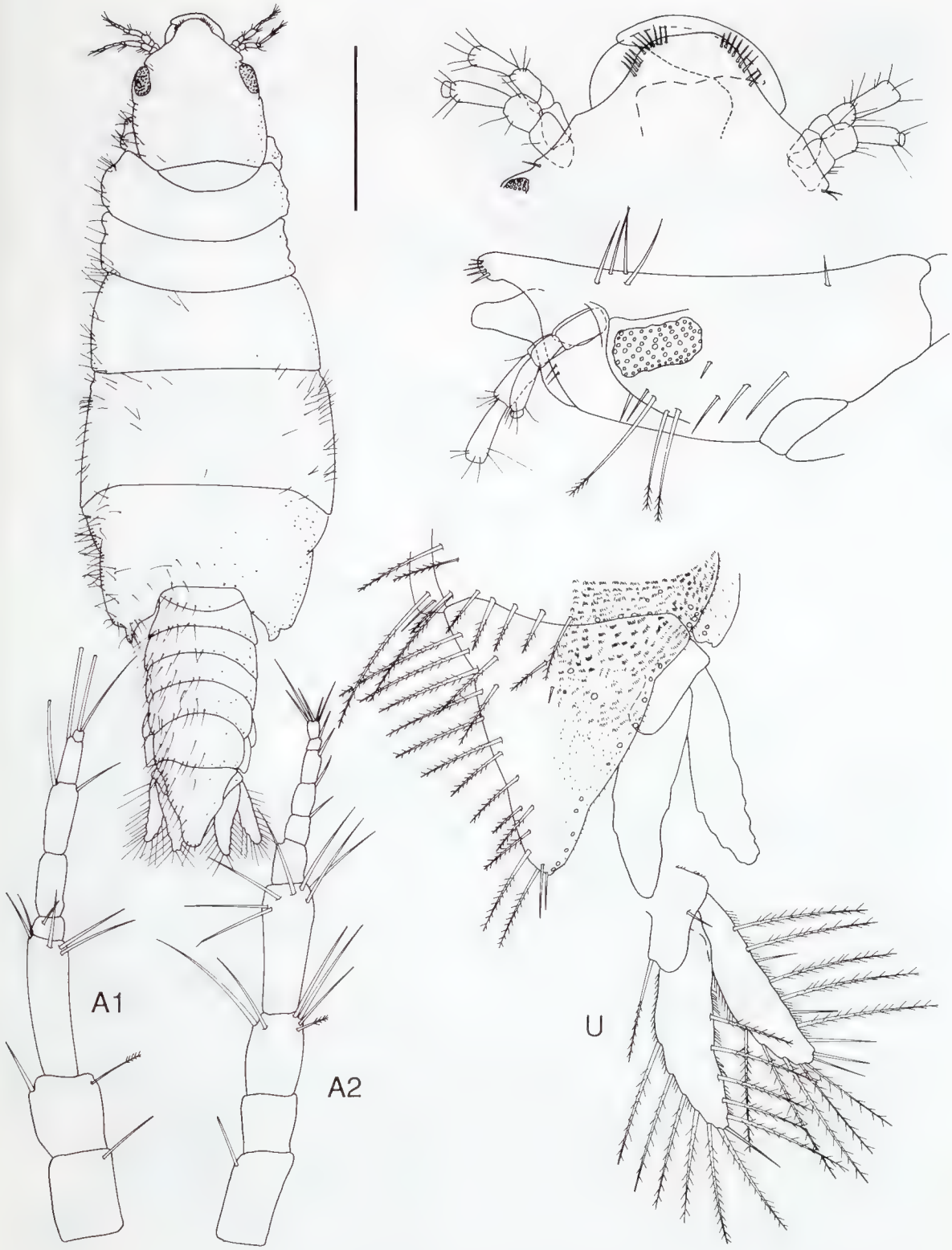


Figure 34. *Caecognathia leptanilla*. Holotype, NMV J27562.

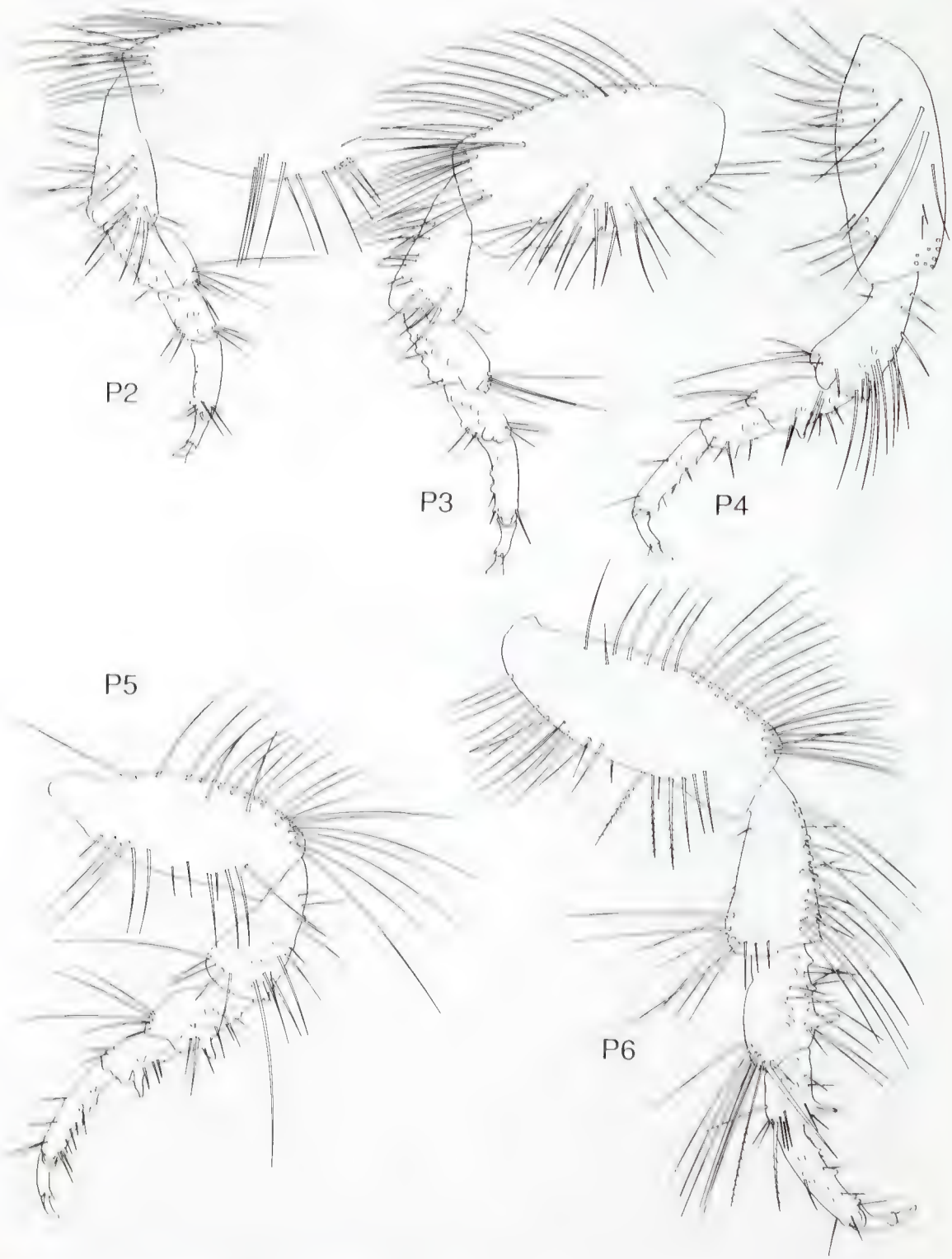


Figure 35. *Caecognathia leptanilla*. Holotype, NMV J27562.

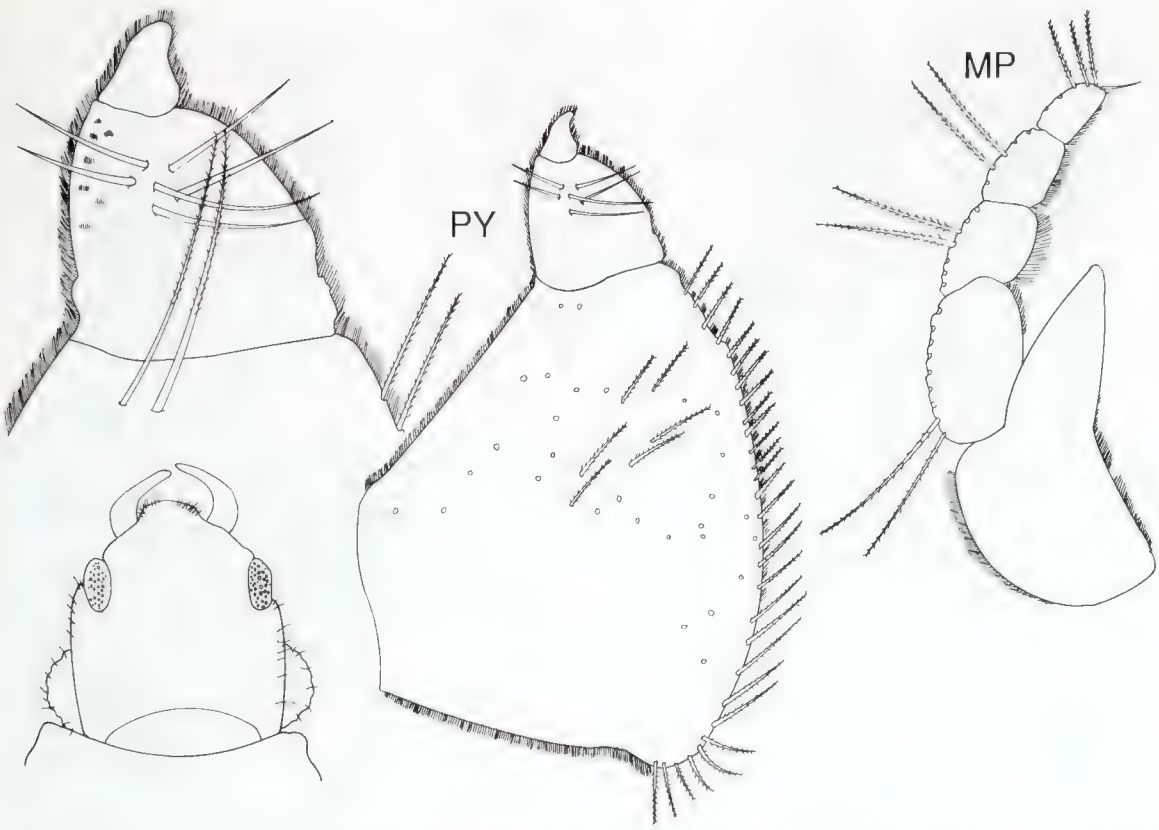


Figure 36. *Caecognathia leptanilla*. Holotype, NMV J27562; Dorsal view of cephalon of paratype, NMV J35492.

and elongate; external margins of articles 2–4 bearing plumose setae; endite clearly reaching article 3, wide. Pylopod 3-articled, internal margin of plumose setae; article 1 with about 35 plumose setae on ventral surface; article 2 conical, proximal margin completely joined to article 1, with 6 setae on ventral surface; article 3 minute.

Pereon width increasing posteriorly; widest at pereonite 5, twice as wide as cephalosome; covered with fine, short setae. Pereonite 1 dorsally reaching lateral margins, divided into 3 regions by posterior margin of cephalosome and partially obscured laterally by pereonite 2. Pereonites progressively longer, except pereonite 2 and 3 subequal. Pereonite 6 posterior border markedly indented; lobuii pronounced, globular. Pereonite 7 very narrow, overlapping pleon. Pleonites progressively longer; pleon tapered, pleonites 1 and 5 narrower than others; pleonal epimera prominent on pleonites 4 and 5. Pleotelson subtriangular, as wide as long, lateral margins slightly sinuous; with 15 pairs of plumose setae laterally and pair of setae on distal apex. Uropodal peduncle with 2 setae; rami subequal, reaching apex of pleotelson, bearing numerous plumose setae.

Pereopods with dense cover of simple setae, particularly on basis; with few lateral projections on anterior faces of ischium to carpus. Pereopods 2 and 3 with broad basis.

Pleopods setose. Pleopod 2 endopod lacking appendix masculina. Penes 2 small contiguous papillae.

*Distribution.* Bass Strait and eastern Tasmania. 27–800 m.

*Remarks. C. leptanilla* is characterised by its produced rostrum.

### ***Caecognathia paratrechia*** sp. nov.

Figures 37–39

*Material examined.* Holotype. South Australia, Pearson I., E side in bay (33°57.30′S, 134°15.70′E), 20 m, bryozoans, sponges etc. on shaded surface, SCUBA,

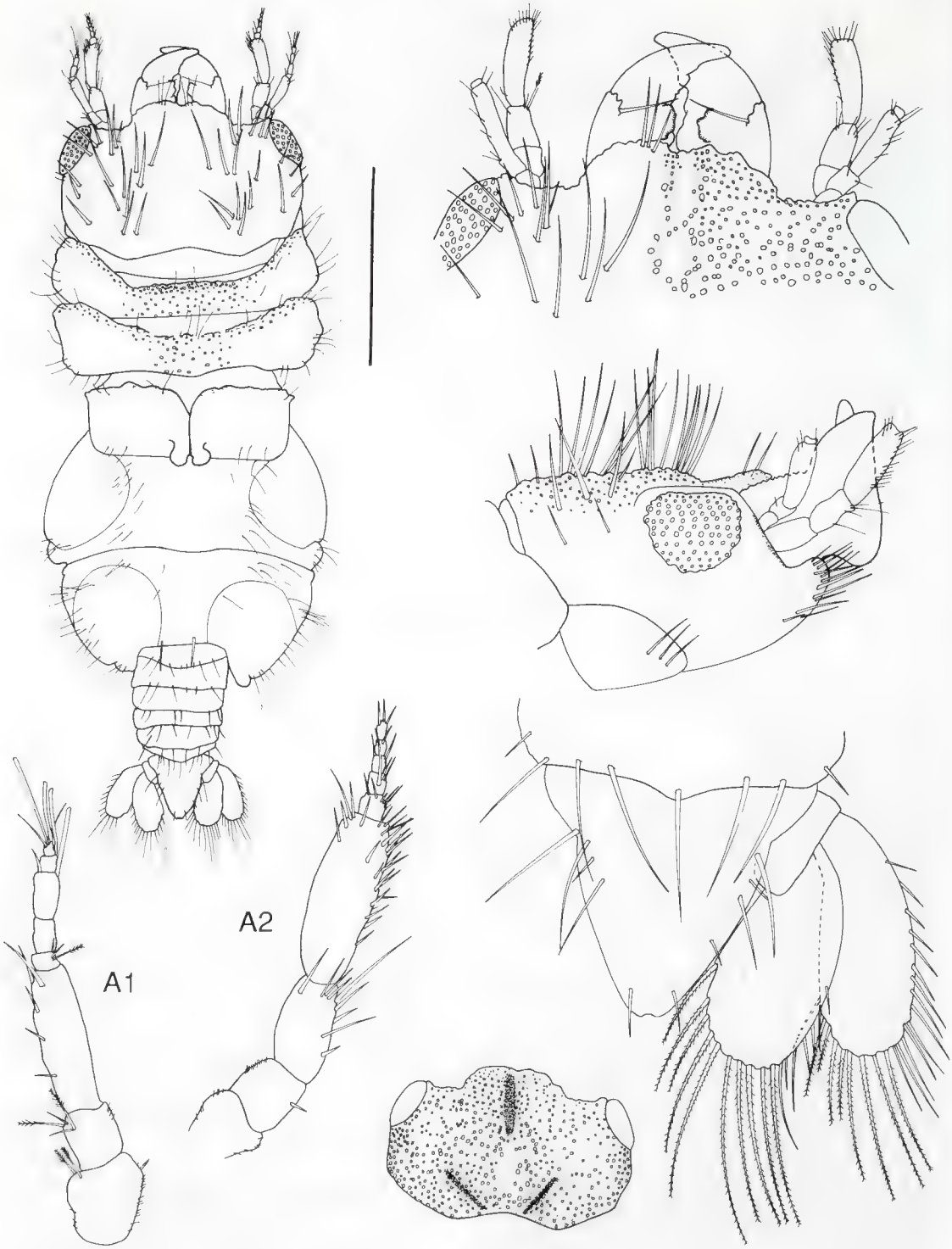


Figure 37. *Caecognathia paratrechia*. Holotype, NMV J27578.

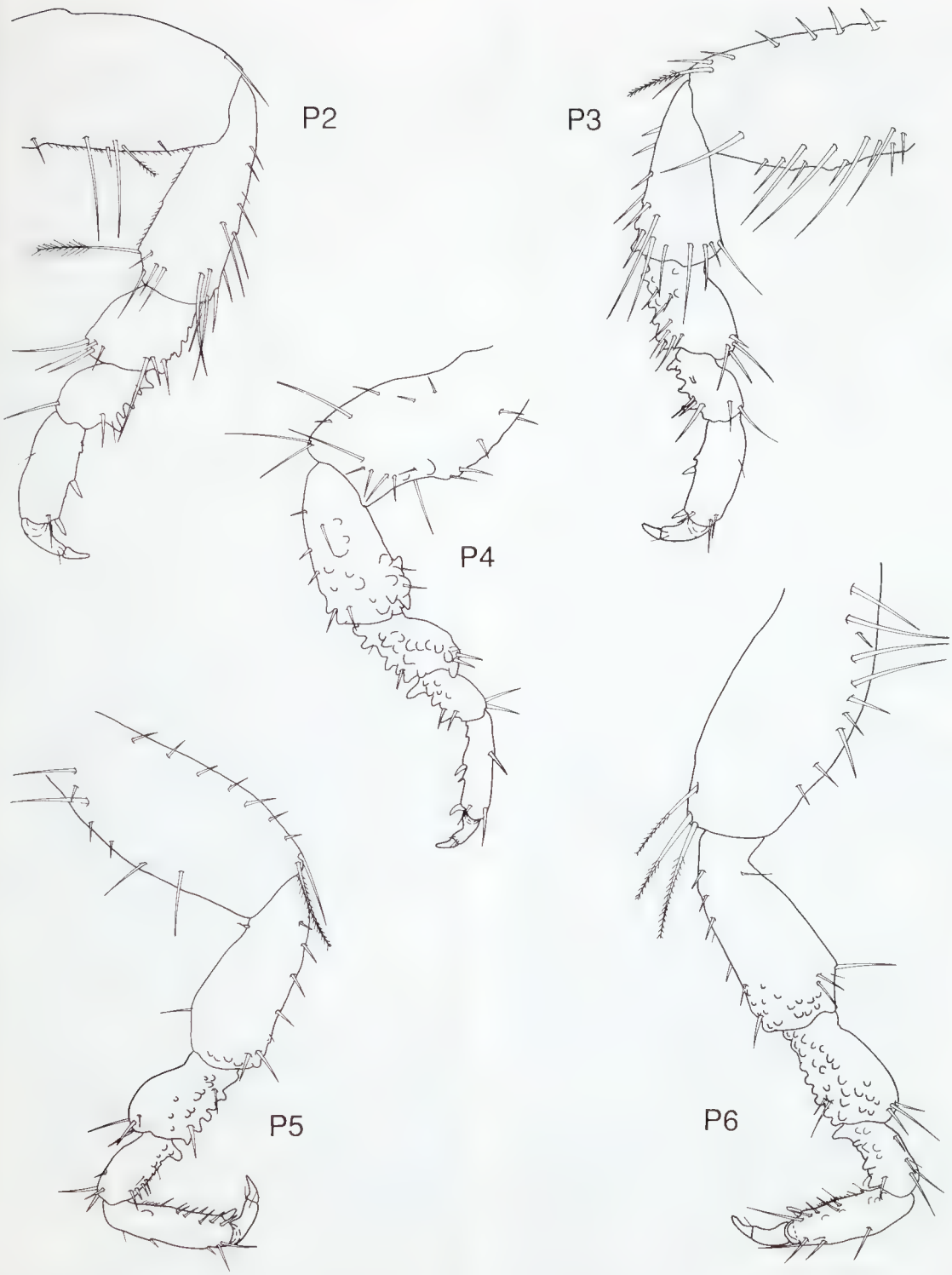


Figure 38. *Caecognathia paratrechia*. Holotype, NMV J27578.

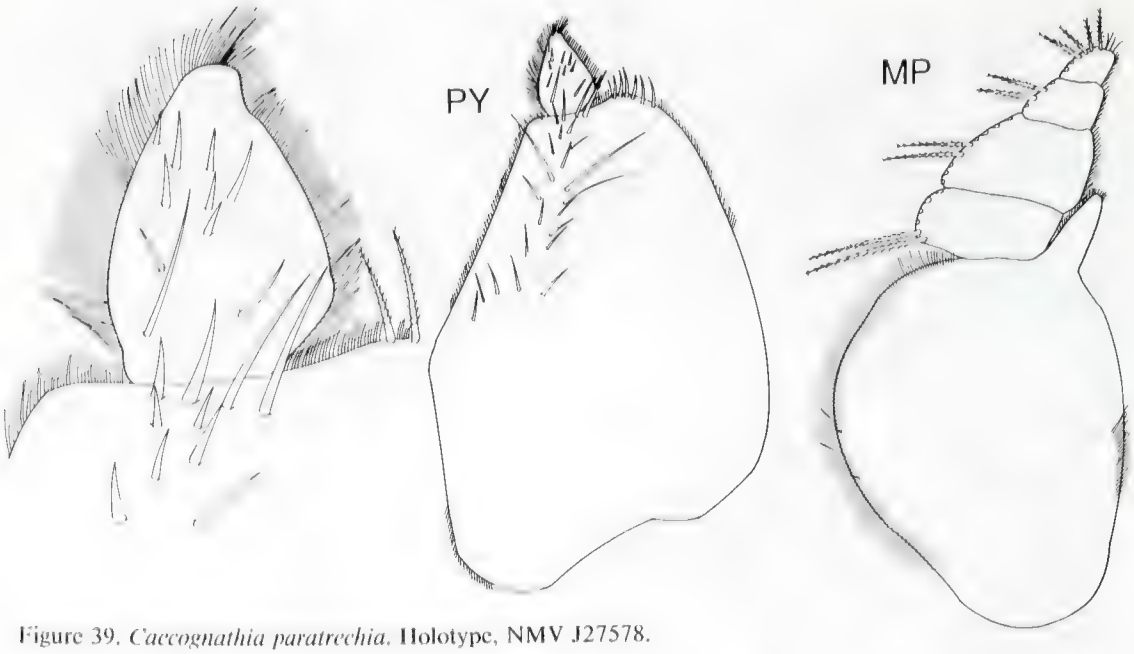


Figure 39. *Caecognathia paratrechia*. Holotype, NMV J27578.

G.C.B. Poore, 17 Apr 1985 (stn SA 55), NMV J27578 (1 male).

*Description*. Total length of holotype: 3.67 mm.

Cephalosome rectangular, 1.5 times as wide as long, lateral margins slightly convex. Eyes well developed, lateral and sessile. Frontal border produced medianly, rounded with irregular border and median indentation; 3 long submarginal setae each side of median indentation. External scissura rounded. Supraocular lobe smoothly convex. Cephalosome with many long simple setae and numerous granules; with mesial furrow and shallower, oblique posterior mesiolateral furrows. Antennae subequal; flagellum of antenna 1 of 5 articles, with 4 aesthetascs, article 3 of peduncle longer than flagellum or peduncle articles 1 and 2 together; flagellum of antenna 2 of 5 articles, flagellum short, shorter than distal article of peduncle. Mandible scoop-shaped, strongly curved, one-third length of cephalosome; with unarmed carina; armed mandibular incisor one-third way along; slightly crenulate blade; setae at base of incisor and prominent quadrate internal lobe at base of mandible. Maxilliped 5-articled; external margins of articles 2–4 bearing plumose setae; endite clearly reaching article 3, narrow. Pylopod 2-articled, internal margin of fine short setae with 6–7 plumose setae on anteromesial margin; article 1 operculate with 23 setae on ventral surface medianly; article 2 conical, with 9–10 setae on ventral surface.

Pereon widest posteriorly at pereonites 5 and 6, 1.2 times as wide as cephalosome; covered with numerous simple setae. Pereonite 1 dorsally reaching lateral margins and partially obscured laterally by pereonite 2. Pereonites 2 and 3 subequal, as wide as cephalon. Pereonite 4 narrow; with anterior constriction; thin median groove and posteriorly directed, bilobed extension of posterior border of pereonite 4. Pereonite 5 and 6 rounded, similar to praniza but not fused. Pereonite 5 with areae laterales. Pereonite 6 with lobi laterales and rounded lobuii. Pereonite 7 not visible. Pleotelson subtriangular, as wide as long; lateral margins sinuous; with 5 pairs of simple setae laterally. Uropodal peduncle without setae; rami rounded, subequal, reaching just beyond apex of pleotelson, bearing numerous plumose setae distally.

Pereopods with few simple setae; with many tubercles on ischium, merus and carpus, particularly on pereopod 4; pereopod 4 smaller than other pereopods.

Pleopods setose. Pleopod 2 endopod lacking appendix masculina. Penes 2 small contiguous papillae.

*Distribution*. SA, rocky habitats, 20 m.

*Remarks*. *C. paratrechia* is characterised by the quadrate mandibular lobe and bilobed posterior projection on pereonite 4.

***Caecognathia trachymesopus*** sp. nov.

Figures 40–42

*Material examined.* Holotype. Tasmania, central Bass Strait, 20 km NNE of North Point (40°32.0′S, 145°23′E), 44 m, muddy shell grit, Smith-McIntyre grab, M.F. Gomon and G.C.B. Poore on FV *Sarda*, 4 Nov 1980 (stn BSS 116), NMV J27571 (1 male).

Paratypes. Collected by M.F. Gomon and G.C.B. Poore on FV *Sarda*, 1980, unless otherwise noted. Tasmania, western Bass Strait, 55 km W of Stokes Point, King I. (40°06′S, 143°16′E), 187 m, fine sand, Smith-McIntyre grab, G.C.B. Poore on HMAS *Kimbla*, 11 Oct 1980 (stn BSS 101), NMV J8310 (1 male). Central Bass Strait, 23 km E of Cape Rochon, Three Hummock I. (40°22.2′S, 145°17′E), 40 m, mainly sand, WHOI epibenthic sled (stn BSS 112), NMV J7799 (2), NMV J7798 (2). 20 km NNE of North Point (40°32.0′S, 145°23′E), 44 m, muddy shell grit, Smith-McIntyre grab (stn BSS 116), NMV J7796 (8). (40°23.8′S, 145°32′E), 66 m, muddy sand, Smith-McIntyre grab (stn BSS 113), NMV J7797 (2). 33 km S of Deal I., (39°48.3′S, 147°19.3′E), 60 m, muddy sand, WHOI epibenthic sled, R.S. Wilson on RV *Tangaroa*, 14 Nov 1981 (stn BSS 161), NMV J8304 (1).

Victoria. Western Bass Strait, 25 km WSW of Cape Otway (38°55′S, 143°25′E), 67 m, medium sand, naturalists' dredge, G.C.B. Poore on HMAS *Kimbla*, 8 Oct 1980 (stn BSS 53), NMV J8309 (1). Central Bass Strait, 60 km SW of Cape Schanck, (39°00.2′S, 144°33.9′E), 74 m, sandy shell, R.S. Wilson on RV *Tangaroa*, 23 Nov 1981 (stn BSS 202), NMV J8307 (2). Eastern Bass Strait, 40 km SSW of Lakes Entrance, Victoria (38°18.0′S, 147°37.0′E), 55 m, muddy fine shell, M.F. Gomon and R.S. Wilson on FV *Silver Gull*, 31 Jul 1983 (stn BSS 209), NMV J8301 (4). Eastern Bass Strait, between Lake Tyers and Pt Ricardo, 21–45 m, sandy sediments, Sep 1990, MSL-EG stns, 10 lots: NMV J24637 (1), NMV J24693 (3), NMV J24638 (1), NMV J24695 (3), NMV J26358 (1), NMV J26359 (2), NMV J26360 (1), NMV J24694 (1), NMV J24640 (1), NMV J24691 (3).

Other material. 11 lots from Bass Strait, 27–293 m depth, NMV collections.

*Description.* Total length of holotype: 3.23 mm.

Brown. Cephalosome elliptical, 1.3 times as long as wide, lateral margins slightly convex. Eyes well developed, lateral and sessile. Frontal border slightly produced, rounded with small median indentation; with 9 submarginal setae each side of indentation, setae generally decreasing in size laterally. External scissura very shallow. Supraocular lobe smoothly convex. Antennae down-turned; antenna 1 slightly longer than antenna 2; flagellum of antenna 1 of 5 articles, with 3 aesthetascs; flagellum of antenna 2 of 4 articles. Mandible strongly curved, half length of cephalosome; with unarmed carina; smooth blade on distal half; basal neck smooth except for 1 rounded, posteriorly directed projection giving an uneven double-scalloped effect; erisma pronounced, covering base of mandible. Maxilliped 5-articled, palp thin and elongate; external margins of articles 2–4 bearing plumose setae; endite clearly reaching article 3, wide. Pylopod 3-articled, internal margin of plumose setae; article 1 with 24 setae on ventral surface; article 2 conical, posterior margin completely joined to article 1, with 5 setae on ventral surface; article 3 minute.

Pereon width increasing posteriorly; widest at pereonite 5, twice as wide as cephalosome; margins with numerous plumose setae. Pereonite 1 dorsally reaching lateral margins, divided into 3 regions by posterior margin of cephalosome and partially obscured laterally by pereonite 2. Pereonites progressively longer; pereonite 6 posterior border markedly indented; lobuii pronounced, globular. Pereonite 7 very narrow, overlapping pleon. Pleon with pleonites subequal, pleonite 5 slightly longer than others. Pleotelson subtriangular, as wide as long; lateral margins sinuous; with 8 pairs of plumose setae laterally and pair of setae on distal apex. Uropodal peduncle with 2 setae; endopod longer than exopod, not reaching apex of pleotelson; internal margins of rami bearing numerous plumose setae.

Basis to carpus of pereopods with dense cover of plumose setae, particularly on basis; with few lateral projections on anterior face of ischium to carpus.

Pleopods setose. Pleopod 2 endopod lacking appendix masculina. Penes 2 small contiguous papillae.

*Distribution.* Bass Strait, 27–293 m.

*Remarks. Caecognathia trachymesopus* is similar to *C. diacamma* but is differentiated by the less produced frontal border, narrower and longer cephalosome, more complex mandible and the lack of lateral sutures on pereonite 6.

***Elaphognathia*** Monod

*Gnathia* (*Elaphognathia*) Monod, 1926: 558–560. — Gurjanova, 1936: 256–257. — Bacescu, 1960: 107–112. — Cals, 1973: 295, 305. — Holdich and Harrison, 1980: 218.

*Type species. Anceus ferox* Haswell, 1885 (herein designated).

*Diagnosis.* Eyes present. Frontal margin of cephalon transverse, deeply excavated; with


Figure 40. *Caecognathia trachymesopus*, Holotype, NMV J27571.

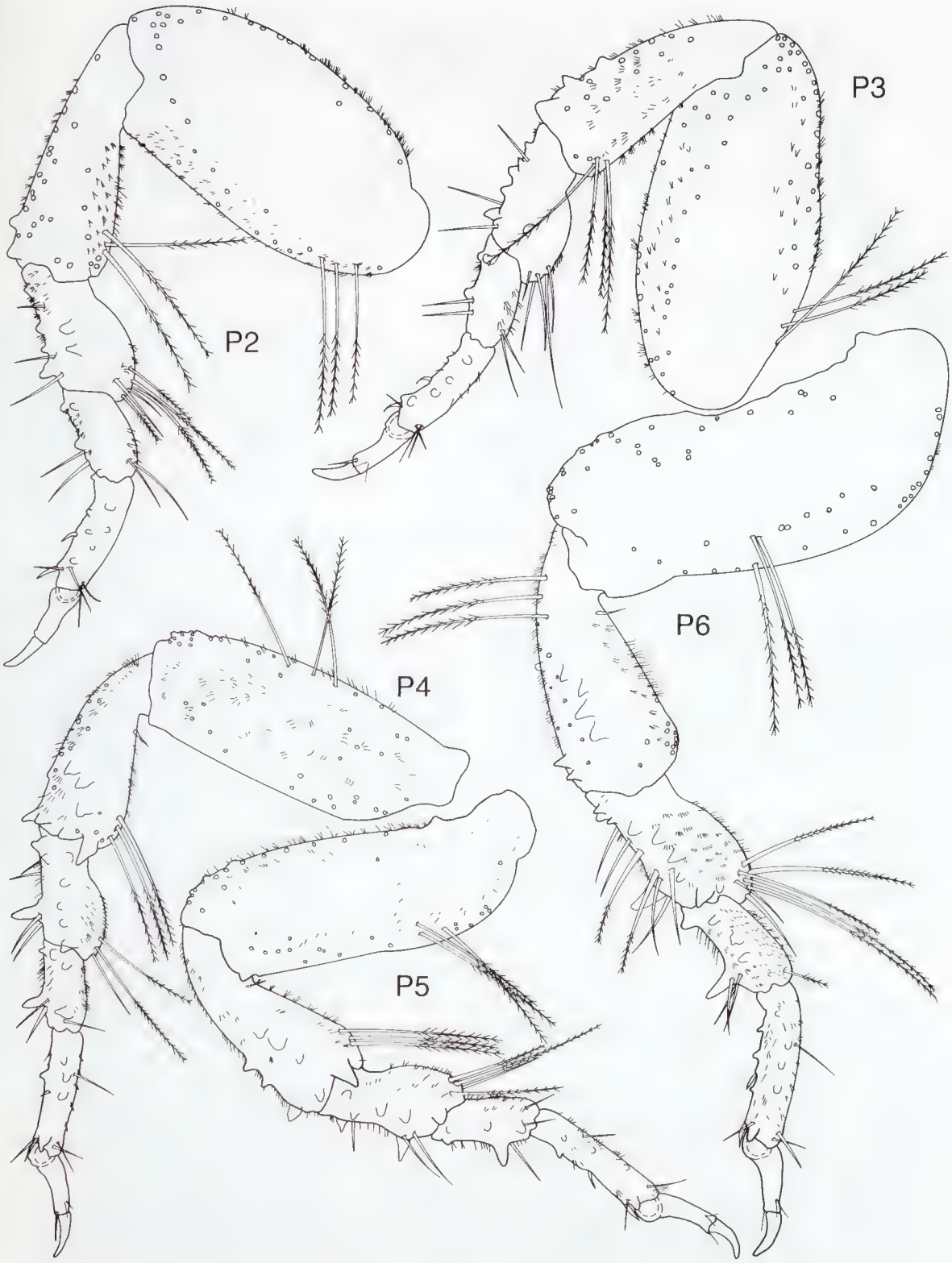


Figure 41. *Caecognathia trachymesopus.* Holotype, NMV J27571.

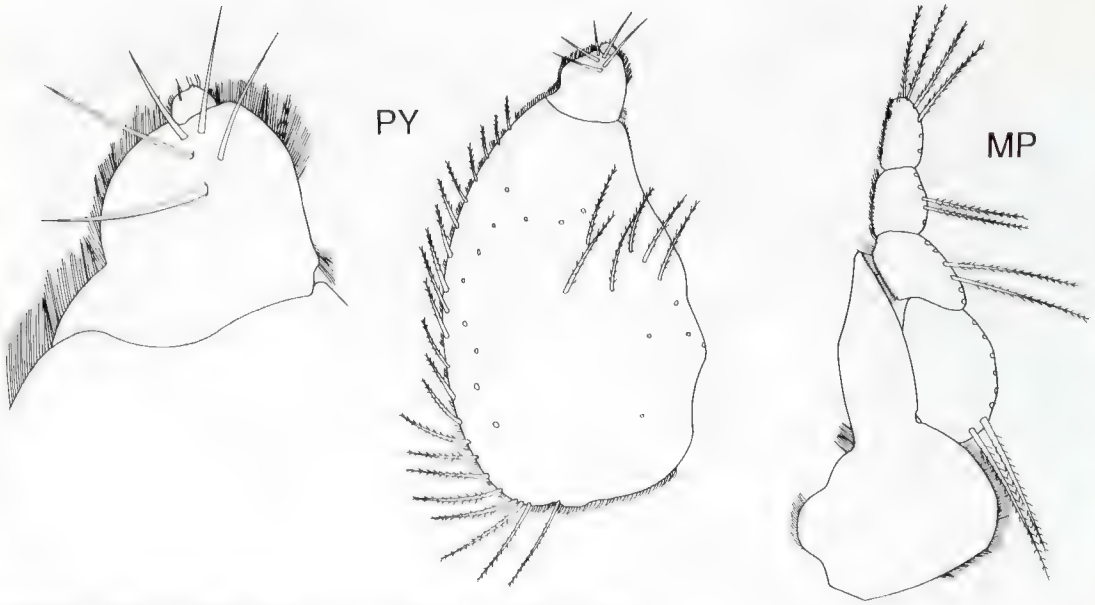


Figure 42. *Caccognathia trachymesopus*. Holotype, NMV J27571.

frontal processes which may be emarginate. Mandibles long, cylindrical; often lacking mandibular blade though may pocess numerous specialised structures. Pereonite 1 immersed in cephalon. Pylopod 2- or 3-articled; operculate, article 1 enlarged, generally with dense external margin of plumose setae; article 3 small or absent.

*Remarks.* The subgenus *Elaphognathia* was erected by Monod (1926) for four species but none was selected as type species, then or since. As the first described *Elaphognathia*, Haswell's Australian species is designated here and the name elevated to generic rank.

Species of *Elaphognathia* are most easily recognised by the excavate frontal border and the elongate mandibles lacking any dentate blade.

The genus was described as Indopacific by Gurjanova (1936) and Bacescu (1960) and Tethyan in origin by Cals (1973). There are 13 species distributed through the Indo-West Pacific and Mediterranean. Of the five species known from Australia, one is newly described. The other four are briefly illustrated (see figs 2N–Q).

**Key to males of Australian species of *Elaphognathia***

1. Supraocular lobe extended dorsally as crest, pereonites 5–6 fused as in pranzia stage ..... *E. rimifrons*

— Supraocular lobe not extended dorsally as crest, pereonites 5–6 not fused ..... 2

2. Mandibles almost twice as long as cephalon, pereonite 1 obvious, pylopods without aerolae ..... 3

— Mandibles as long as cephalon, pereonite 1 not visible, pylopods with aerolae ..... 4

3. Mandibles with conical internal lobe at base, without small internal notch behind tip; mediofrontal process with 3 setae either side of median notch and not produced beyond base of mandibles ..... *E. froygattella*

— Mandibles with large quadrate internal lobe at base and small internal notch behind tip; mediofrontal process produced beyond base of mandibles with 2 acute lateral projections, no setae ..... *E. bifurcilla*

4. Mandibles cylindrical, with 2–3 apical cusps; cephalon without low median tubercle; pylopod 3-articled, with 2 plumose setae on anterior margin of article 1 (NB: specimens can lack the slight median projection found at the base of the rounded excavation of the frontal border, a characteristic used in previous keys) ..... *E. ferox*

— Mandibles with small blade, lacking apical cusps; cephalon with low median tubercle; pylopod 2-articled, article 1 with many plumose setae on margin ..... *E. forceps*

***Elaphognathia froygattella*** sp. nov.

Figures 43–45

*Material examined.* Holotype. Victoria, western Bass Strait, 35 km SSW of Cape Otway (39°07.0'S, 143°14.6'E), 84 m, coarse sand, WHOI epibenthic sled, R.S. Wilson on RV *Tangaroa*, 20 Nov 1981 (stn BSS 183), NMV J27568 (1 male).

Paratypes. Type locality, NMV J8374 (2 males).

*Description.* Total length of holotype: 5.09 mm.

Cephalosome rectangular, twice as wide as long, lateral margins convex. Eyes well developed, lateral and sessile. Frontal border deeply excavated mid-dorsally; mediofrontal process inferior, ventral to excavation, conical with large median notch, with 6 setae spread across base of notch; superior frontolateral process acute, directed anterolaterally, located at base of mandible, with 4 evenly spread setae on both margins. Inferior frontolateral process acute. External scissura very shallow. Supraocular lobe very low, acute. Antenna 1 directed ventrally in lateral view; flagellum of 5 articles, with 4 aesthetascs. Antenna 2 twice as long as antenna 1; flagellum of 7 articles. Mandible straight, twice as long as cephalosome; cylindrical, with no obvious blade; with unarmed carina and 2 conical internal lobes; distal lobe, one-third way along, directed anteriorly; proximal lobe, at base of mandible, directed posteriorly. Maxilliped 5-articled, endite clearly reaching article 3; palp broad with articles 2–5 wider than long, external margins bearing plumose setae. Pylopod 3-articled; article 1 with 4 setae on ventral surface medianly, distal internal margin bearing plumose setae; article 2 circular with 3 setae on ventral surface distally; article 3 minute.

Pereon evenly sided, as wide as cephalosome, margins with numerous setae. Pereonite 1 barely reaching lateral margins dorsally, partially obscured laterally by pereonite 2; pereonites 2 and 3 subequal, 4 wider than 5 and 6. Pereonite 7 not visible. Pleon broad, epimera prominent. Pleonites 2–4 subequal, pleonite 5 shorter than others. Pleotelson subtriangular, wider than long, lateral margins sinuous; with 3–5 pairs of simple setae. Uropodal peduncle with 3 setae; rami subequal, reaching beyond the apex of pleotelson, bearing numerous plumose setae distally.

Pereopods progressively longer, with dense cover of simple setae. Pereopod 6 with one anterior spiniform seta on merus,

Pleopods setose. Pleopod 2 endopod lacking appendix masculina. Penes 2 small contiguous papillae.

*Distribution.* Western Bass Strait, 84 m.

*Remarks. Elaphognathia froygattella* is most similar to *E. bifurcilla* Holdich and Harrison from North Queensland, particularly in overall body proportions; the great length of the mandibles and their more lateral attachment. *E. froygattella* differs from *E. bifurcilla* in the smaller emarginate mediofrontal process, absence of an internal notch near the tip of the mandible and the different internal mandibular lobe.

***Euneognathia*** Stebbing

*Euneognathia* Stebbing, 1893: 338. — Monod, 1926: 312–313 (and other authors).

*Type species. Anceus gigas* Beddard, 1886 (monotypy).

*Diagnosis.* Eyes present. Frontal margin of cephalon not produced; transverse, with frontal processes. Mandibles with blade and pseudoblade. Cephalon with paraocular ornamentation. Pereonite 1 immersed in cephalon. Posterior margin of pereonite 6 deeply excavated for pleon. Pylopod 5-articled; not operculate, with dense external margin of plumose setae.

*Remarks. Euneognathia* is a monotypic genus found around Antarctica (Schultz, 1978). It is the only genus of Gnathiidae with the combination of frontal processes and a 5-articled, nonoperculate pylopod. *Euneognathia gigas* is a very large species, males being greater than 10 mm long. The species' status as member of a

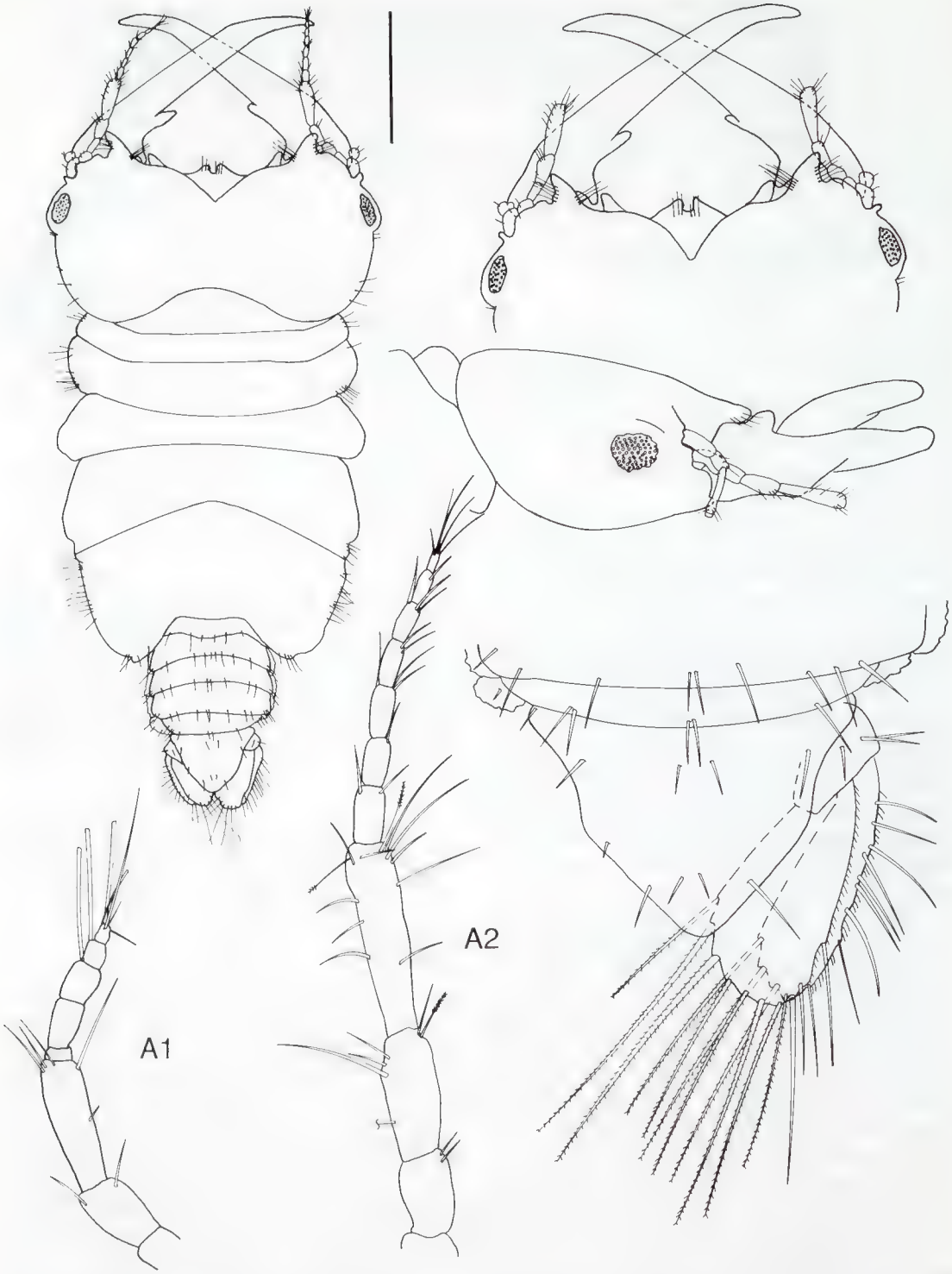


Figure 43. *Elaphognathia froygattella*. Holotype, NMV J27568.

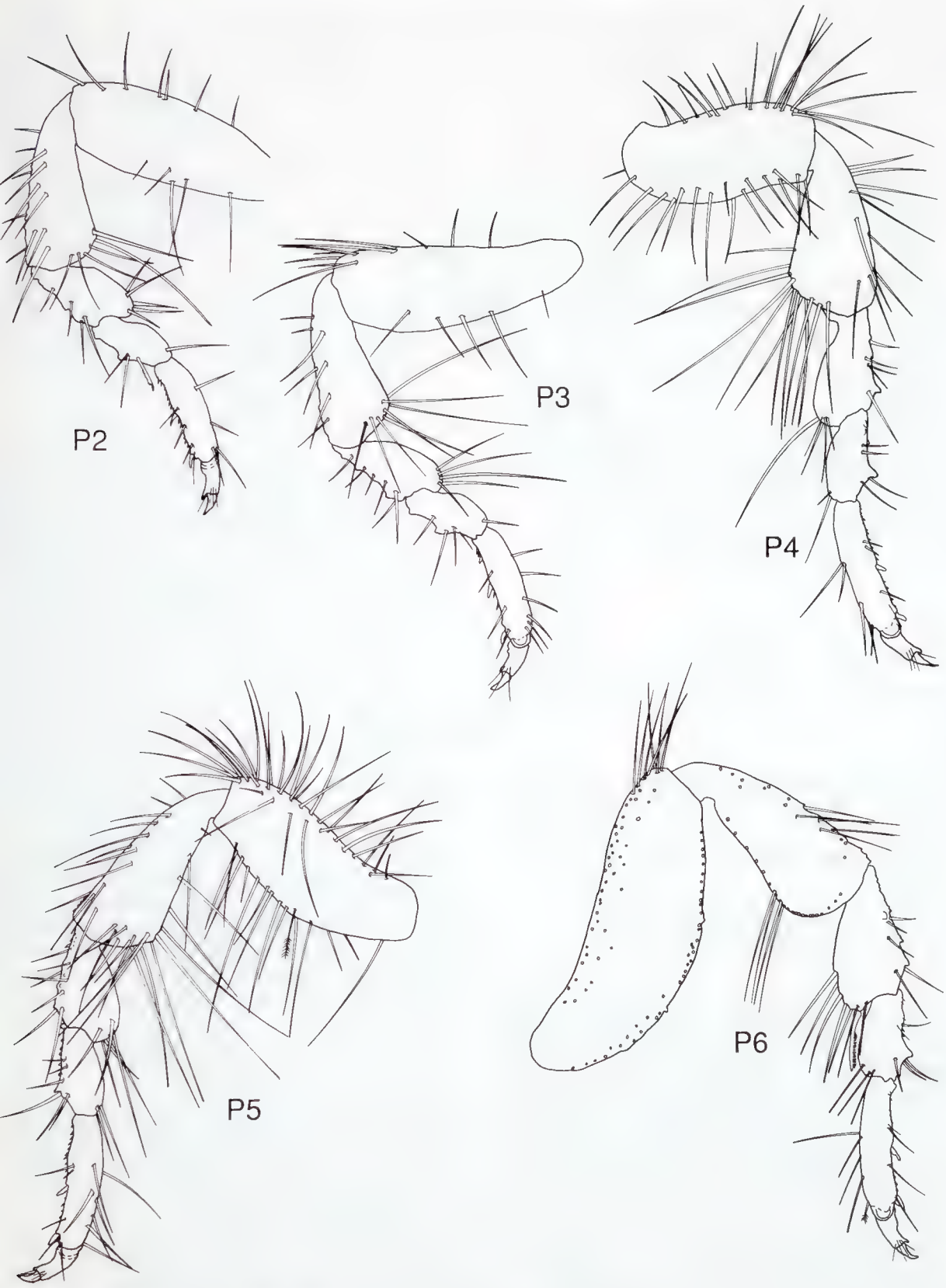


Figure 44. *Elaphognathia froygattella.* Holotype, NMV J27568.

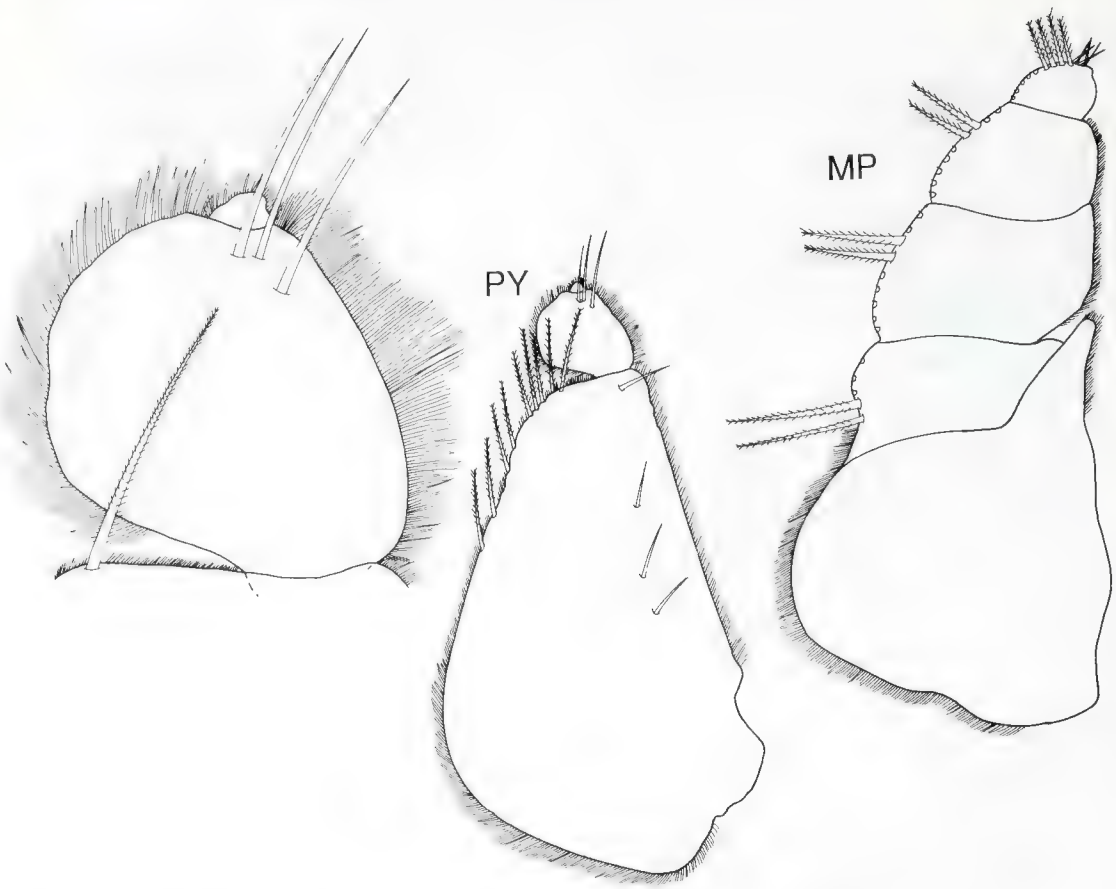


Figure 45. *Elaphognathia froygattella.* Holotype, NMV J27568.

monotypic genus is supported by the phylogenetic analysis.

### ***Gibbagnathia*** gen. nov.

*Type species. Gibbagnathia europalothrix* sp. nov.

*Diagnosis.* Eyes present. Frontal border slightly produced. Mandibles simple, lacking distinct blade. Antenna 1 with stout peduncle. Mouthparts small; pylopod pediform and maxilliped of 2 articles. Pereon rectangular, with numerous setae and small granules; pereonite 3 with large anteriorly directed projection; pereonite 7 visible. Pleon wide, with prominent epimera.

*Etymology.* From *gibba* (Latin), meaning a hump, referring to the dorsal prominence on pereonite 3 and *Gnathia.*

*Remarks. Gibbagnathia* is a monotypic genus confined to Bass Strait, the only species being *G. europalothrix.* It is most easily distinguished from other Gnathiidae by the large anteriorly directed projection orginating dorsally from pereonite 3. *Gibbagnathia* and *Thaumastognathia* both have reduced maxillipeds and small, pediform pylopods but differ largely in the shape of the pereon and mandibles.

### ***Gibbagnathia europalothrix*** sp. nov.

Figures 46, 47

*Material examined.* Holotype. Tasmania, eastern Bass Strait, 30 km N of North Point, Flinders I., (39°26.3′S, 147°48.7′E), 49 m, medium sand, WHOI epibenthic sled, R.S. Wilson on RV *Tangaroa,* 17 Nov 1981 (stn BSS 173), NMV J8366 (1 male).

Paratypes. Tasmania, western Bass Strait, 48 km NNW of Cape Farewell, King I. (39°22′S, 143°28′E), 104 m, medium sand, carbonate, G.C.B. Poore on HMAS *Kimbla,* 10 Oct 1980 (stn BSS 78), NMV J8369 (2). 47 km NW of Cape Farewell, King I. (39°20′S, 143°34′E), 95 m, coarse sand, carbonate, G.C.B. Poore

on HMAS *Kimbla*, 10 Oct 1980 (stn BSS 77), NMV J8368 (1 male). Central Bass Strait, 44 km NE of Cape Wickham, King I. (39°22.0'S, 144°18.3'E), 60 m, coarse sand, R.S. Wilson on RV *Tangaroa*, 23 Nov 1981 (stn BSS 203), NMV J8365 (1 male). Eastern Bass Strait, 30 km N of North Point, Flinders I., (39°26.3'S, 147°48.7'E), 49 m, medium sand, Smith-McIntyre grab, R.S. Wilson on RV *Tangaroa*, 17 Nov 1981 (stn BSS 173), NMV J8367 (1 male).

Victoria. Western Bass Strait, 30 km SSW of Warrnambool, (38°38.2'S, 142°35.0'E), 59 m, WHOI epibenthic sled, R.S. Wilson on RV *Tangaroa*, 20 Nov 1981 (stn BSS 188), NMV J8370 (1 male). Eastern Bass Strait, 19.1 km W of Pt Ricardo (37°50.57'S, 148°25.02'E), 36 m, sand-shell, Smith-McIntyre grab, Marine Science Laboratories on FV *Sarda*, 26 Sep 1990 (stn MSL-EG 43), NMV J24633 (1 male).

*Description.* Total length of holotype: 2.03 mm.

Cephalosome rectangular, 2.4 times as wide as long, lateral margins straight. Cephalosome and anterior pereon covered with numerous setae. Eyes well developed, lateral and sessile, not easily visible dorsally. Frontal border slightly produced medianly, with 6 setae submarginally, in 2 clumps of 3. Lamina dentata visible, external scissura very shallow. Supraocular lobe not pronounced dorsally, raised in lateral view as distinct projection. Antennae stout, antenna 2 longer than antenna 1; flagellum of antenna 1 of 4 articles, with 3 aesthetascs, peduncle articles slightly rounded; flagellum of antenna 2 of 5 articles. Mandible located on median projection; close set, straight; half length of cephalosome; dorsoventrally flattened; thin and flexible in preserved specimens without obvious blade or features, raised in lateral view. Maxilliped very reduced, of 2 articles with 4 setae distally. Pylopod thin, elongate, 4-articled, all with seta, terminal article minute.

Pereon evenly sided, as wide as cephalosome, covered with numerous simple setae except for pereonite 5. Pereonite 1 dorsally small, not reaching lateral margins and partially obscured laterally by pereonite 2. Pereonite 2 slightly produced anterolaterally. Pereonite 3 with large, distinct anteriorly directed, bilobed projection partially overhanging pereonites 1 and 2. Pereonite 4 with narrow anterior constriction. Pereonite 6 posterior border deeply concave, with large extensions lateral to pleon. Pereonite 7 very narrow, overlapping pleon. Pleon wide except pleonite 1 which is constrained by pereonite 6; pleonite 2 three-quarters width of pereon; pleonites 3–5 decreasing in width posteriorly. Pleotelson subtriangular, wider than long, lateral margins sinuous with 1 pair of simple setae laterally and pair of setae on distal apex. Uropodal peduncle without setae; endopod twice as long as exopod, reaching beyond apex of pleotelson; rami bearing numerous plumose setae distally.

Pereopods with moderate cover of plumose and simple setae, plumose setae confined mainly to basis and ischium; pereopods 2 and 6, larger than pereopods 3–5, with setae scales on ischium.

Pleopods setose. Pleopod 2 endopod lacking appendix masculina. Penes fused as 1 small papilla.

*Distribution.* Bass Strait, 36–104 m depth.

*Remarks. G. europalothrix* has similar mouthparts to species of *Thaumatognathia* but differs by possessing a rectangular pereon with a deeply concave posterior border, straight pleon with pronounced epimera and straight mandibles without a distinct blade. *G. europalothrix* is most easily identified by the very large anteriorly directed projection on pereonite 3.

### ***Gnathia*** Leach

*Gnathia* Leach, 1814: 386, 402. — Monod, 1926: 326–329 (part) and numerous other authors.

*Anceus* Risso, 1816: 8 (type species: *Anceus forficularius* Risso, 1816).

*Praniza* Latreille, 1817: 54 (type species: *Oniscus marinus* Slabber, 1778).

*Zuphea* Risso, 1826: 104 (type species: *Zuphea spariçola* Risso, 1826).

*Gnathia* (*Gnathia*) s.s. — Monod, 1926: 329 (part).

*Gnathia* (*Perignathia*). — Monod, 1926: 554–555 (not *Perignathia* Monod, 1922).

*Type species. Gnathia termitoides* Leach, 1814 (= *Cancer maxillaris* Montagu, 1804) (monotypy)

*Diagnosis.* Eyes usually present. Frontal margin of cephalon generally transverse, with frontal processes. Mandibles usually with dentate mandibular blade and mandibular incisor. Cephalon may possess paraocular ornamentation and/or a dorsal sulcus. Pereonite 1 immersed in cephalon. Pylopod 2- or 3-articled; operculate, article 1 enlarged, generally with dense external margin of plumose setae; article 3 small or absent.

*Remarks.* The genera *Anceus*, *Praniza*, and *Zuphea*, are all based on European gnathiid larval stages whose specific identities are impossible to confirm (Monod, 1926). They have therefore traditionally been treated as junior

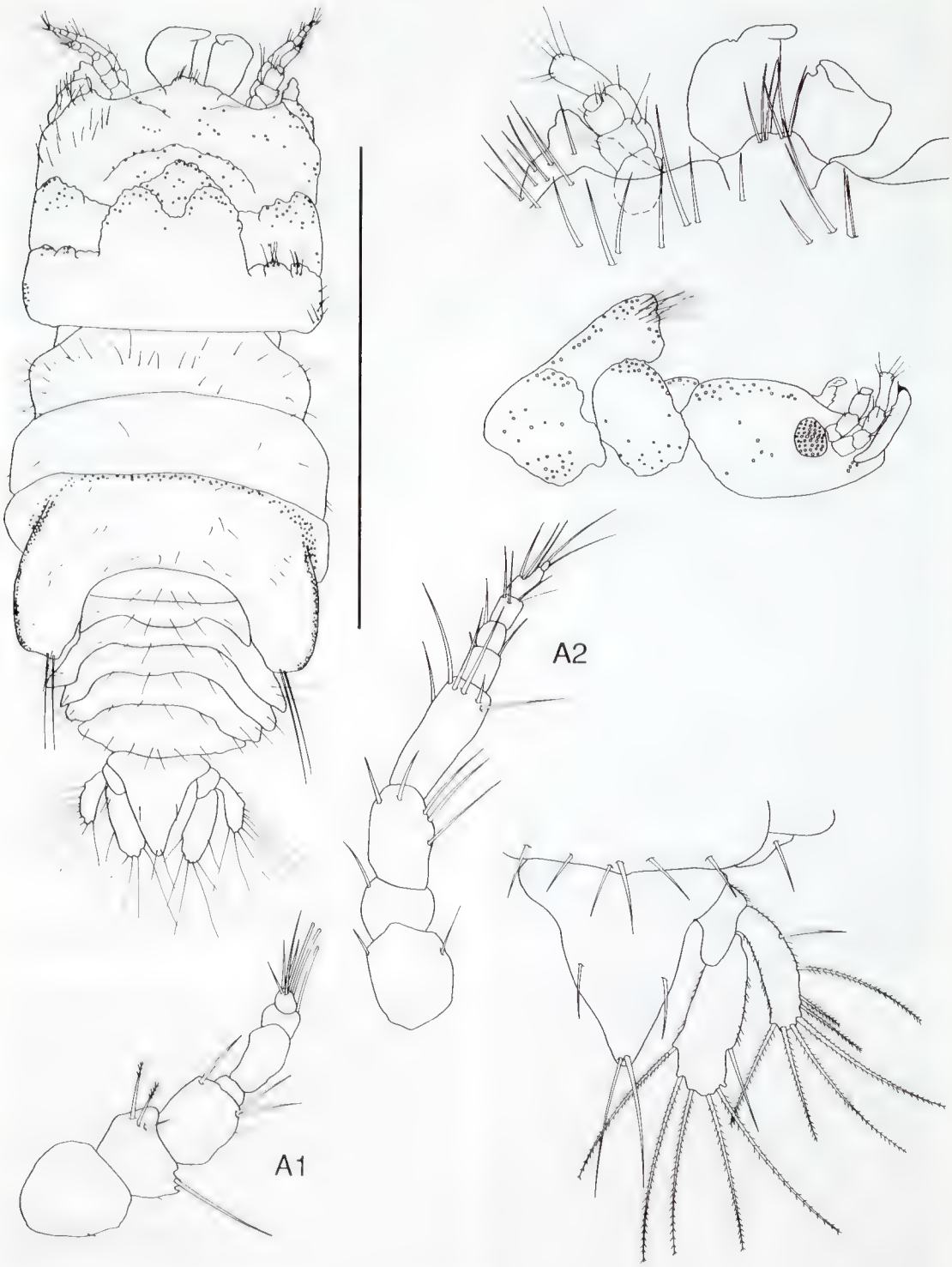


Figure 46. *Gibbagnathia europalothrix*. Holotype, NMV J8366.

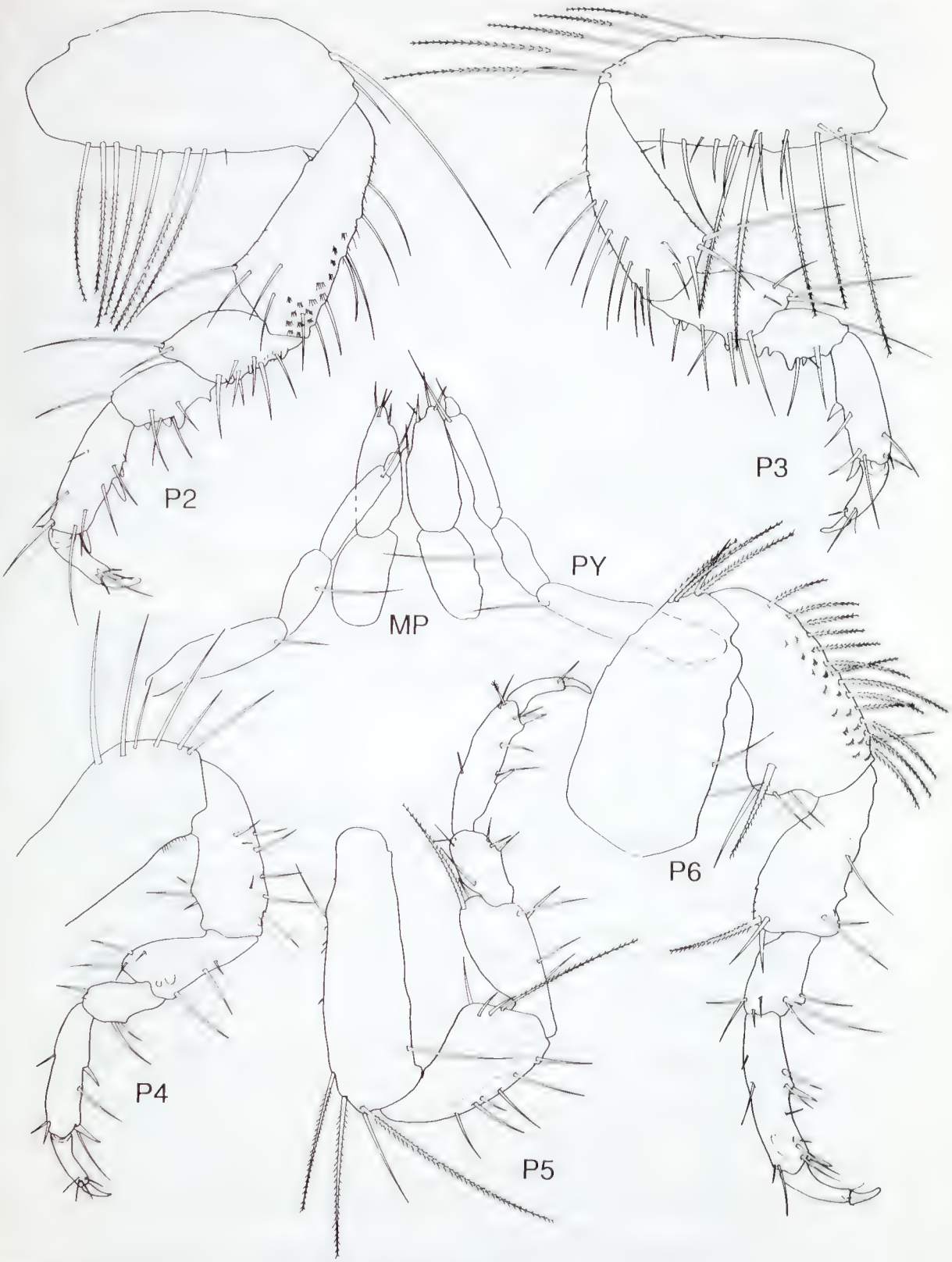


Figure 47. *Gibbagnathia europalothrix*. Holotype, NMV J8366.

synonyms of *Gnathia* and, in the case of *Praniza*, as the name for the larval stage of all gnathiids.

Our concept of *Gnathia* is narrower than that of Monod (1926). A fifth generic name treated as a junior synonym by him, *Caecognathia* Dollfus, 1901, is herein revived for a monophyletic group of species once placed in *Gnathia* but now considered the sister taxon of *Gnathia* + *Elaphognathia*. Wägele (1987) proposed that *Heterognathia* Amar and Roman, 1974 is a junior synonym of *Gnathia* but with the restriction of the generic concept it becomes a junior synonym of *Caecognathia* instead.

*Elaphognathia* Monod, 1926, hitherto a subgenus, is elevated to generic rank.

*Perignathia* Monod, 1922 is problematical name. It was erected as a genus for *Anceus abyssorum* Sars, a species we believe to be a member of *Caecognathia* Dollfus and could therefore be its junior synonym. Later, Monod (1926) admitted that the material on which he based his generic diagnosis was not Sars' species and he reidentified it as *Gnathia fallax* Monod, 1926, a member of *Gnathia* s.s. The type species is therefore subject to dispute and can only be decided by reference to the ICZN. As long as the name is viewed as a junior synonym its type species is of little consequence. Monod (1926) further complicated the issue by excluding both potential type species from *Perignathia* and using it as a subgeneric name for another, *Gnathia triospathiona* Boone, 1918. If this species were to warrant generic or subgeneric status it would require a new generic name but our analysis suggests that this is not so.

*Gnathia* is the largest genus in the family whose species are recognised by the possession of a broad 2- or 3-articled pylopod, presence of frontal processes, a straight frontal border, and non-elongate mandibles with dentate blade. We are unable to find a unifying synapomorphy of *Gnathia* but treat it as a paraphyletic taxon formed by the exclusion of species of the monophyletic *Elaphognathia* from a larger clade. Eleven species from Australia have already been described (see Table 5) and are briefly figured (see fig. 2).

**Key to males of species of *Gnathia* from Australia**

1. Cephalon with a very large tubercle in anterior midline and 2 smaller tubercles near base of the mandibles. Paraocular ornamentation a single tubercle anterior to oblique ridge of 3 small tubercles ..... *G. mulieraria*

— Cephalon not so ..... 2

2. Penes fused and produced ..... 3

— Penes not fused and produced ..... 4

3. Penes very large, directed posteriorly; mediofrontal process sharply conical; pylopod 2-articled with 3 areolae on article 1 ..... *G. falcipenis*

— Penes small, directed anteriorly; mediofrontal process rounded with 2 setae each side; pylopod 3-articled, with 2 areolae ..... *G. epopostruma*

4. Dorsum dived by shallow grooves marked by lines of chromatophores; paraocular ornamentation as a mediolateral ridge, eyes overhanging in lateral view ..... *G. cornuta*

— Cephalon not so ..... 5

5. Pleopods unequal, anterior pair naked, 2–3 times the size of the 3 setose posterior pairs ..... *G. variobranchia*

— Pleopods subequal ..... 6

6. Paraocular ornamentation present ..... 7

— Paraocular ornamentation absent ..... 13

7. Pylopod lacking internal margin of plumose setae, length greater than twice width ..... 8

— Pylopod with internal margin of plumose setae, length about twice the width ..... 9

8. Superior frontolateral process large and circular, lacking setae; mandibular blade slightly crenulate ..... *G. prolasius*

— Superior frontolateral processes small and conical, with many setae; mandibular blade smooth ..... *G. stigmacros*

9. Inferior frontal border relatively straight, crenulate ..... *G. meticola*

— Frontal border with mediofrontal process ..... 10

10. Paraocular ornamentation extremely pronounced, particularly in lateral view; frontal border produced; maxillipedal endite narrow . *G. notostigma*

— Paraocular ornamentation not extremely produced; frontal border at most only slightly produced; maxillipedal endite broad ..... 11

11. Mandibles slightly asymmetrical, lacking incisor, less than half length of cephalon; mediofrontal process superior; pereon without anterior constriction on peronite 4 ..... *G. calamitosa*

— Mandibles symmetrical, with incisors, greater than half length of cephalon; mediofrontal process inferior; pereon with anterior constriction on peronite 4 ..... 12

12. Cephalon and anterior pereon with granules; mandibles with pseudoblade; pylopod with areolae; mediofrontal process conical with many notches on lateral margins ..... *G. campontus*

— Cephalon and pereon without granules; mandibles lacking pseudoblade; pylopod with areolae; mediofrontal process truncate; dorsal sulcus on peronite 5 ..... *G. biorbis*

13. Mandibles without incisors ..... 14

— Mandibles with incisors ..... 17

14. Frontal border produced ..... 15

— Frontal border not produced ..... 16

15. Mandibles with dorsal lobe; frontal border lacking setae . *G. rhytidoponera*

— Mandibles without dorsal lobe; frontal border with 8–9 setae in row, each side of mediofrontal process ..... *G. halei*

16. Peronite 1 not visible; mandibles inflected upwards at 90°; mediofrontal process bifid; sparsely setose ..... *G. mystrium*

— Peronite 1 visible; mandibles not inflected; mediofrontal process trifid; heavily setose ..... *G. iridomyrmex*

17. Mediofrontal border smooth ..... *G. asperifrons*

— Mediofrontal border of cephalosome, between mandibles, markedly toothed or notched ..... 18

18. Mediofrontal process trifid, half length of superior frontolateral process ..... *G. calmani*

— Mediofrontal process a single projection, as long as superior frontolateral processes ..... 19

19. Mandible with mandibular seta, lacking pseudoblade; pleopods without setae; dorsally setose; pereon without granules; cephalon rectangular ..... *G. odontomachus*

— Mandible lacking mandibular seta, with pseudoblade; pleopods setose; not dorsally setose; cephalon and anterior pereon with granules; cephalon quadrate ..... *G. latidens*

### *Gnathia camponotus* sp. nov.

Figures 48–50

*Material examined.* Holotype. Tasmania, eastern Bass Strait, 100 km NE of North Point, Flinders I. (38°52.6′S, 148°25.2′E), 130 m, fine sand, WHOI epibenthic sled, R.S. Wilson on RV *Tangaroa*, 15 Nov 1981 (stn BSS 170), NMV J27566 (1 male).

Paratypes. Type locality, NMV J8322 (20 males). 37 km NNE of Eddystone Point (40°40.7′S, 148°36.9′E), 67 m, muddy sand, WHOI epibenthic sled, R.S. Wilson on RV *Tangaroa*, 14 Nov 1981 (stn BSS 164), NMV J8327 (3 males). 70 km ENE of North Point, Flinders I. (39°28.4′S, 148°41.8′E), 110 m, coarse sand, naturalists' dredge, G.C.B. Poore on HMAS *Kimbla*, 28 Mar 1979 (stn BSS 35), NMV J8331 (1).

Victoria, eastern Bass Strait, 43 km SE of Port Albert (38°53.7′S, 147°06.5′E), 58 m, coarse shell, Smith-McIntyre grab, R.S. Wilson on RV *Tangaroa*, 18 Nov 1981 (stn BSS 177), NMV J8323 (3). 50 km SE of Port Albert (38°54.3′S, 147°13.4′E), 58 m, coarse shell, WHOI epibenthic sled, R.S. Wilson on RV *Tangaroa*, 18 Nov 1981 (stn BSS 176), NMV J8330 (3). 40 km SSW of Lakes Entrance (38°18.0′S, 147°37.0′E), 55 m, muddy fine shell, WHOI epibenthic sled, M.F. Gomon and R.S. Wilson on FV *Silver Gull*, 31 Jul 1983 (stn BSS 209), NMV J8328 (3).

Other material. Bass Strait, 44–115 m, NMV J8325 (1); NMV J8324 (7); NMV J8332 (4). NMV J8329 (2); NMV J8326 (2).

*Description.* Total length of holotype: 3.36 mm.

Cephalosome quadrate, lateral margins convex. Numerous very fine granules on cephalosome and anterior pereon. Eyes well developed, lateral and sessile. Frontal border transverse; mediofrontal process inferior, conical with marked notches and 2 long setae laterally; superior frontolateral process smoothly conical, half length of mediofrontal process. Lamina dentata visible. External scissura very shallow. Supraocular lobe not pronounced, ventral accessory supraocular less rounded. Cephalosome with broad dorsal sulcus; paraocular tubercles and setae; with small posterior median tubercle at base of sulcus; with translucent elliptical region anteromedianly, above buccal cavity. Antenna 2 longer than antenna 1; flagellum of antenna 1 of 5 articles, with 2 aesthetases; flagellum of antenna 2 of 7 articles. Mandible straight, two-thirds length of cephalosome; with unarmed carina; slight mandibular incisor halfway along; ventral dentate blade on distally half, with smooth pseudoblade dorsally; internal lobe on proximal half a long crenulate lamina; basal neck short. Maxilliped 5-articled; external margins of articles 2–4 bearing plumose setae; endite barely reaching article 3. Pylopod 3-articled, internal margin of plumose setae; article 1 with 3 areolae along internal margin, with 13 setae distally on ventral surface and along external margin; article 2 with 4 setae distally on ventral surface; article 3 minute.

Pereon evenly sided, as wide as cephalosome. Pereonite 1 dorsally reaching lateral margins, divided into 3 regions by posterior margin of cephalosome and partially obscured laterally by pereonite 2 and cephalon. Pereonites 2 and 3 subequal; 4 with anterior constriction; 5 and 6 together longer than others together. Pereonite 7 very narrow, overlapping pleon. Pleonites progressively narrower after pleonite 2, pleonal epimera prominent on pleonites 4 and 5. Pleotelson subtriangular, as wide as long, with 2 pairs of simple setae and pair of setae on distal apex. Uropodal peduncle with 3 setae; rami subequal, reaching apex of pleotelson; rami bearing numerous plumose setae distally.

Pereopods of typical gnathiid form with few simple setae.

Pleopods setose. Pleopod 2 endopod with appendix masculina half length of rami. Penes 2 small contiguous papillae.

*Distribution.* Bass Strait, 55–130 m depth.

*Remarks.* This species most closely resembles *G. latidens* (Beddard) from north-eastern Australia. These two species are characterised by an inferior conical mediofrontal process which is wider than long and a smaller superior frontolateral processes.

*G. camponotus* differs from *G. latidens* in possessing a regularly notched mediofrontal process, a small tubercle on the posterior cephalon and paraocular ornamentation.

### *Gnathia epopostruma* sp. nov.

Figures 51–53

*Material examined.* Holotype. Victoria, western Bass Strait, 44 km SW of Cape Otway (39°06.3′S, 142°55.6′E), 81 m, medium sand, R.S. Wilson et al. on RV *Tangaroa*, 21 Nov 1981 (stn BSS 192), NMV J8373 (1 male).

*Description.* Total length of holotype: 3.83 mm.

Specimen damaged, missing left mandible and slightly deformed. Cephalosome quadrate, lateral margins straight. Eyes well developed, lateral and sessile. Frontal border produced; mediofrontal process superior, rounded with 2 setae laterally; superior frontolateral process conical, with 4–5 setae on external margin. External scissura very shallow. Supraocular lobe

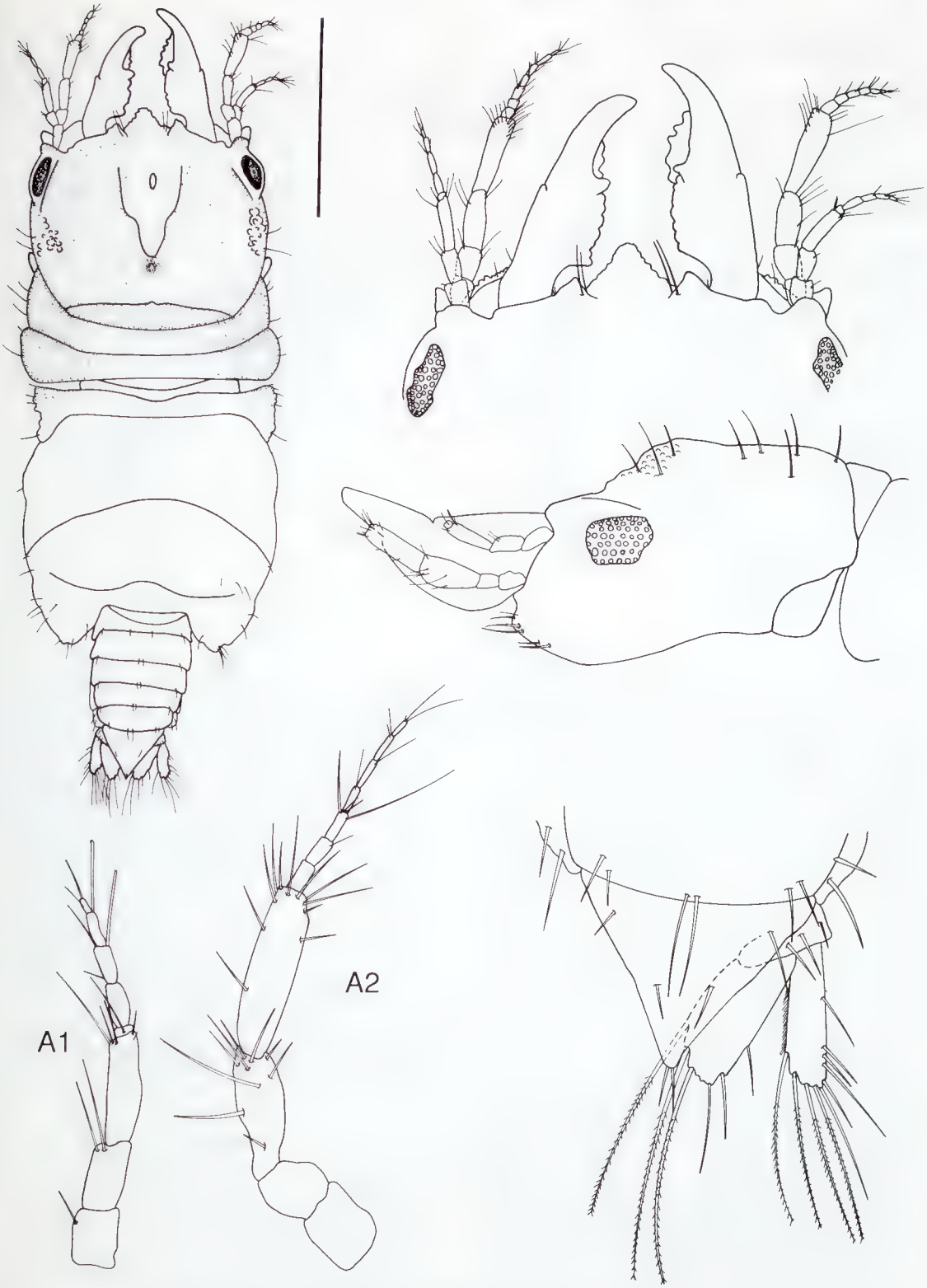


Figure 48. *Gnathia camponotus.* Holotype, NMV J27566.

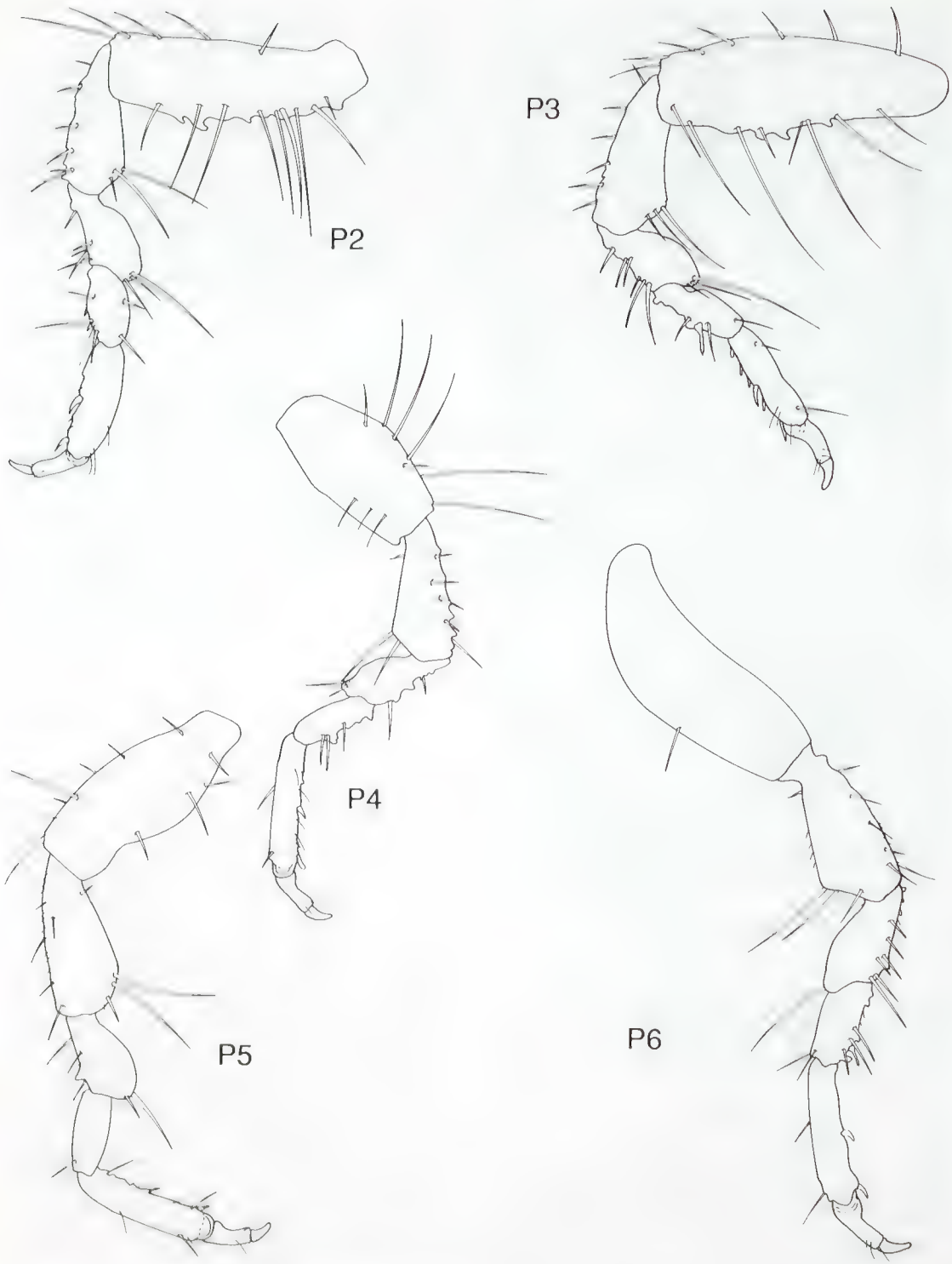


Figure 49. *Gnathia camponotus*. Holotype, NMV J27566.

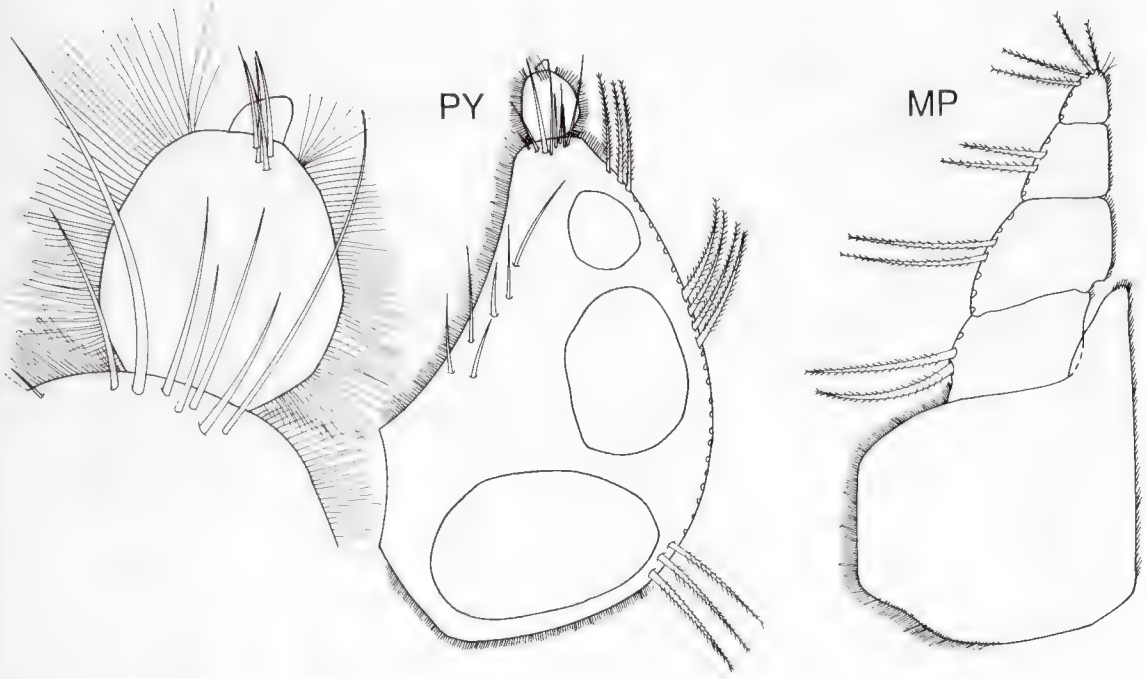


Figure 50. *Gnathia camponotus*. Holotype, NMV J27566.

not pronounced. Cephalosome with short, broad dorsal sulcus; crenulate paraocular ridge partially obscuring eyes. Antennae normal; antenna 2 twice as long as antenna 1; flagellum of antenna 1 of 5 articles, with 1 aesthetasc; flagellum of antenna 2 of 7 articles. Mandible raised distally, subequal to length of cephalosome; with long, acute apex, one-third length of mandible; unarmed carina and lacking incisor; seta at midpoint; with crenulate blade in middle third; proximally with internal lobe a crenulate lamina; basal neck obvious. Maxilliped 5-articled; external margins of articles 2–4 bearing plumose setae; maxilliped endite clearly reaching article 3, narrow. Pylopod 3-articled, internal margin of plumose setae; article 1 with 2 small areolae and 8 setae on ventral surface, 6 distally; article 2 with 8 setae on ventral surface; article 3 minute.

Pereon widest anteriorly, as wide as cephalosome; covered with numerous simple setae. Pereonite 1 dorsally small, not reaching lateral margins and partially obscured laterally by pereonite 2. Pereonite 2 and 3 subequal; pereonite 4 with anterior constriction; pereonite 6 longest. Pereonite 7 very narrow, overlapping pleon. Pleonites subequal, pleonal epimera prominent. Pleotelson subtriangular, as wide as long, lateral margins sinuous; with 3 pairs of simple setae and pair of setae on distal apex. Uropodal peduncle with 4 setae; rami subequal, reaching beyond apex of pleotelson; internal margins of rami bearing numerous plumose setae.

Pereopods subequal, with moderate cover of simple setae; pereopod 2 with 1 posterior pectinate seta on carpus; posterior margin of merus of pereopods 5 and 6 with row of short, fine setae.

Pleopods setose. Pleopod 2 endopod lacking appendix masculina. Penes prominent, present as 2 large papillae.

*Distribution.* Western Bass Strait, 81 m depth.

*Remarks. Gnathia epopostruma* is most similar to *G. falcipenis* Holdich and Harrison. Both species possess a trifid, produced frontal border; raised paraocular ornamentation and similarly proportioned cephalon and pereon. *G. epopostruma* differs in having a rounded, not sharply conical mediofrontal process; a more hirsute habitus; paraocular ornamentation which overhangs the eyes; and smaller, though still enlarged, anteriorly directed penes. The penes of *G. falcipensis* are posteriorly directed.

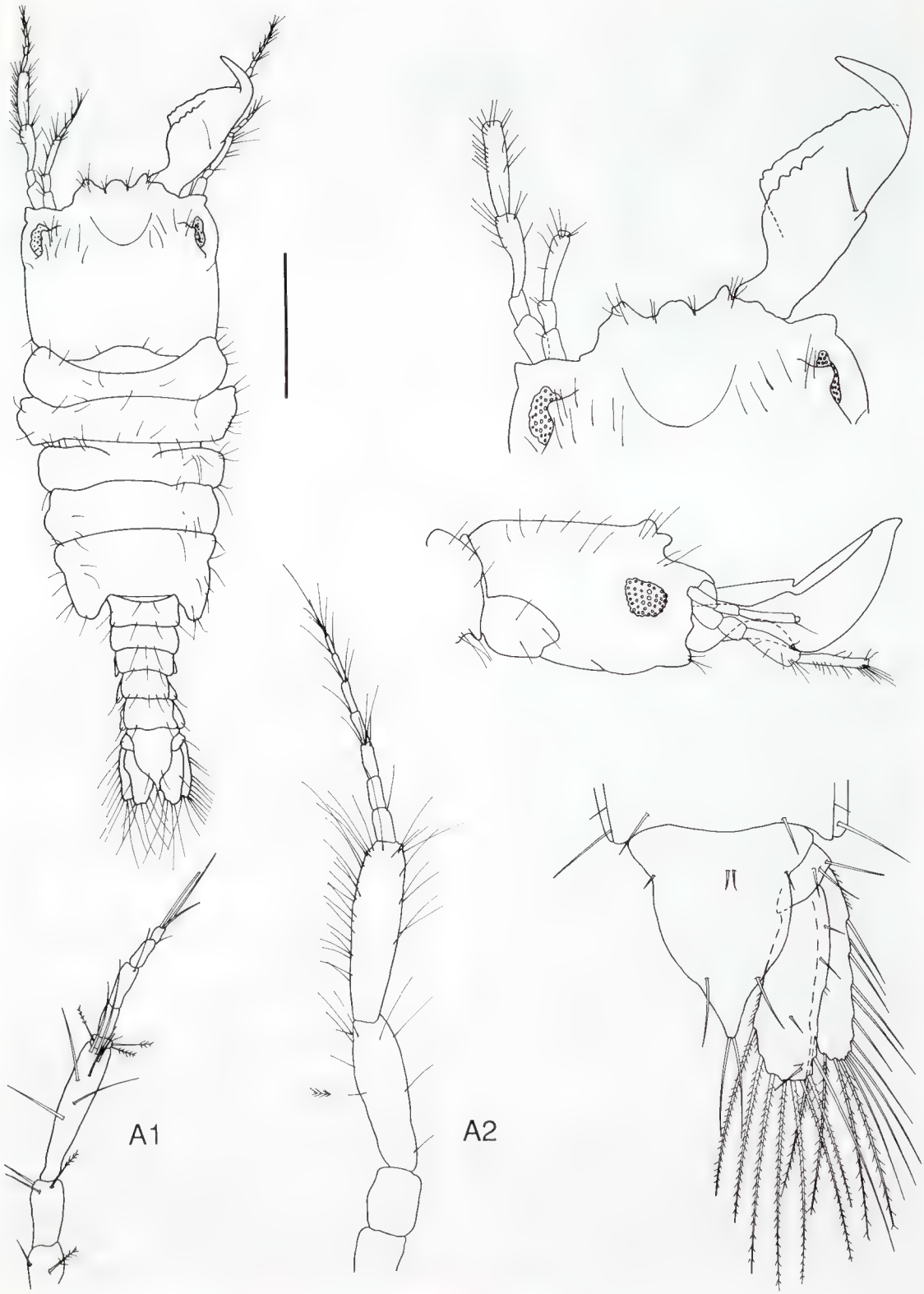


Figure 51. *Gnathia epopostruma*. Holotype, NMV J8373.

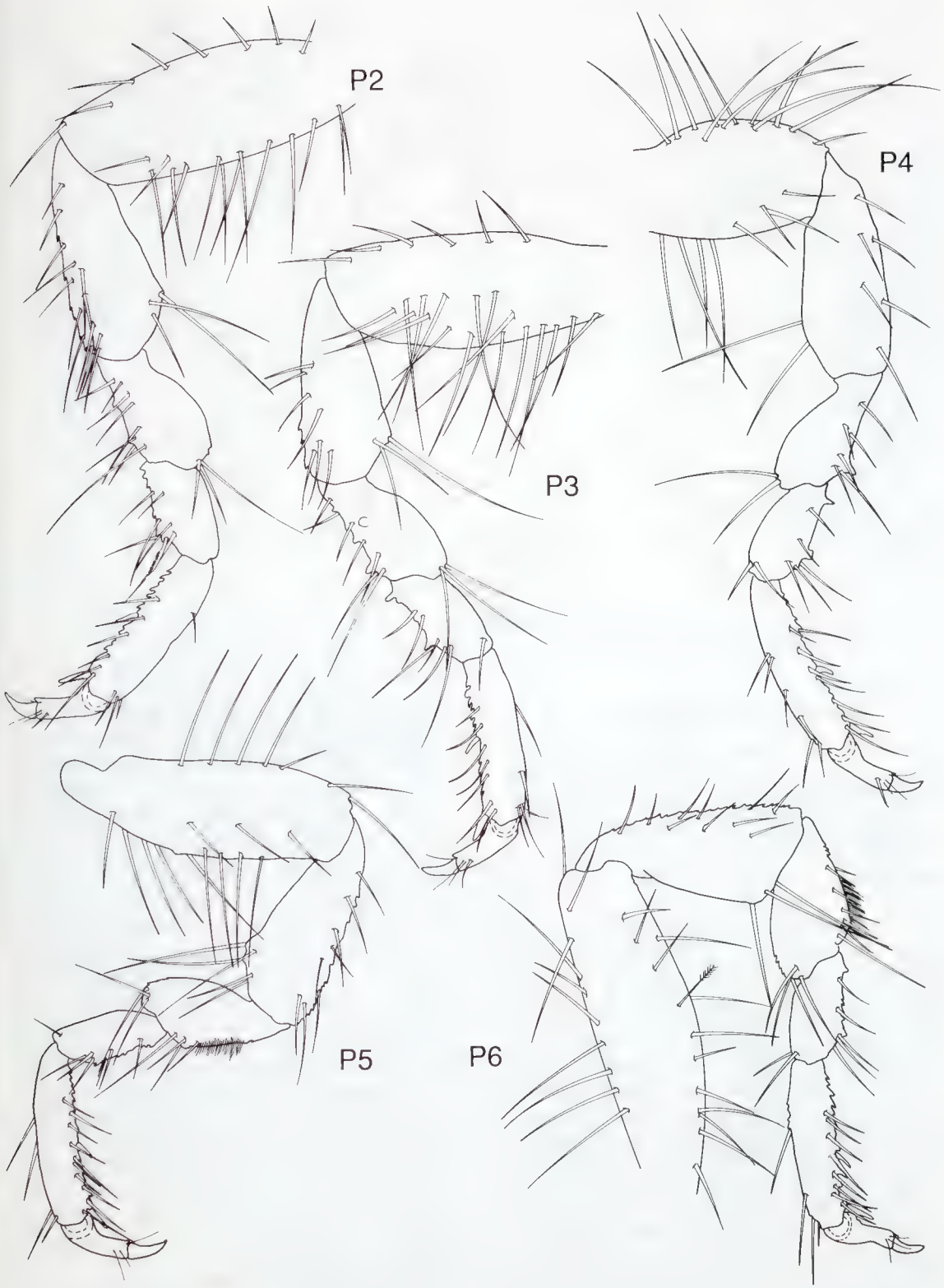


Figure 52. *Gnathia epopostruma.* Holotype, NMV J8373.

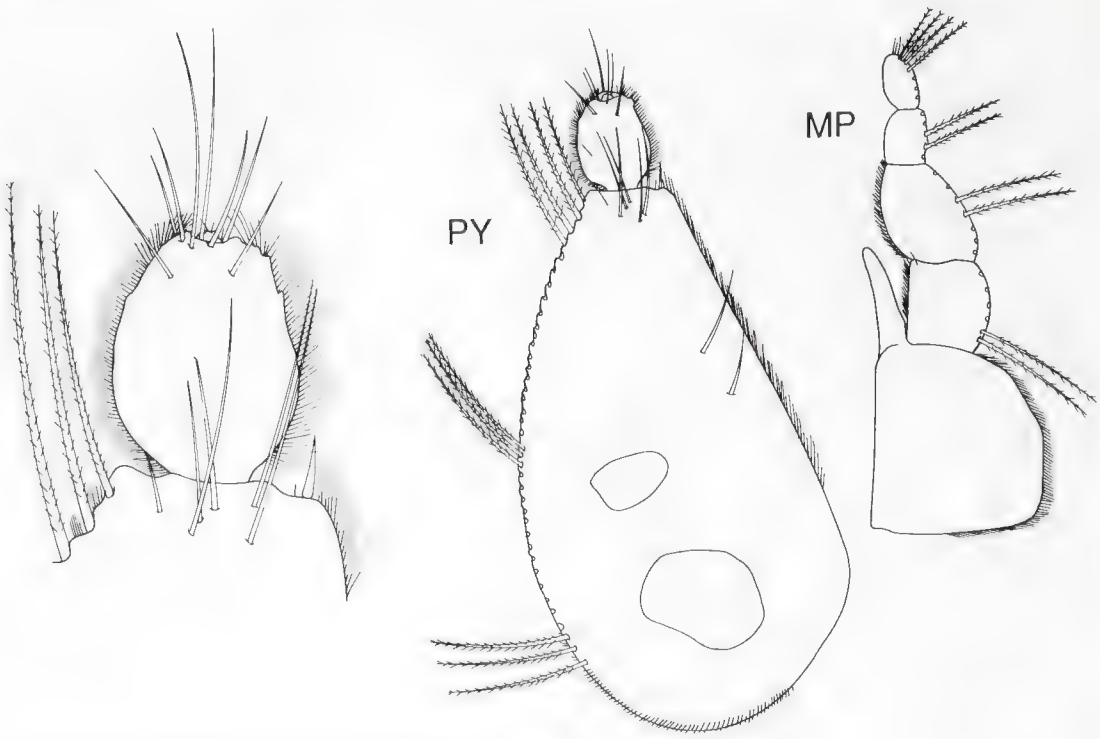


Figure 53. *Gnathia epopostruma*. Holotype, NMV J8373.

***Gnathia iridomyrmex*** sp. nov.

Figures 54–56

*Material examined.* Holotype. Victoria, Saxon Reef, Portland (38°18.5′S, 141°38.5′E), 11 m, red coralline alga turf, SCUBA airlift, R.S. Wilson, 5 Mar 1992 (stn CRUST 178), NMV J27572 (1 male).

*Description.* Total length of holotype: 2.52 mm.

Preserved specimen dark brown. Cephalosome rectangular, 1.15 times as wide as long, lateral margins slightly convex. Eyes well developed, lateral and sessile. Frontal border transverse. Mediofrontal process inferior, broad, trifid. Superior frontolateral process acute, directed anterolaterally, twice length of mediofrontal process with 4 setae evenly spaced on internal margin. External scissura rounded. Supraocular lobe not pronounced. Cephalosome with small dorsal sulcus; translucent elliptical region anteromedial above buccal cavity. Antenna 2 longer than antenna 1; flagellum of antenna 1 of 5 articles, with 3 aesthetascs, distal peduncle article longer than 2 proximal articles; flagellum of antenna 2 of 7 articles. Mandible straight, two-thirds length of cephalosome: with unarmed carina; without incisura; seta at midpoint, irregularly crenulate blade on proximal two-thirds with short basal neck. Maxilliped 5-articled; external margins of articles 2–4 bearing plumose setae; endite barely reaching article 3. Pylopod 3-articled, internal margin of plumose setae; article 1 with 3 areolae and 3 setae on ventral surface distally; article 2 with 4 setae on ventral surface; article 3 minute.

Pereon widest anteriorly, as wide as cephalosome; covered with numerous plumose setae. Pereonite 1 dorsally small, not reaching lateral margins and partially obscured laterally by pereonite 2. Pereonite 2 and 3 subequal; pereonite 4 narrower than others, with anterior constriction; pereonite 5 and 6 longest. Pereonite 7 very narrow, overlapping pleon. Pleonite 5 shorter than others, pleonal epimera prominent. Pleotelson subtriangular, as wide as long; lateral margins sinuous; with 3 pairs of simple setae and pair of setae on distal apex. Uropodal peduncle with 2 setae; rami subequal, reaching beyond apex of pleotelson; internal margins of rami bearing numerous plumose setae.

Pereopods subequal, with moderate cover of simple setae and crenulate anterior margin of

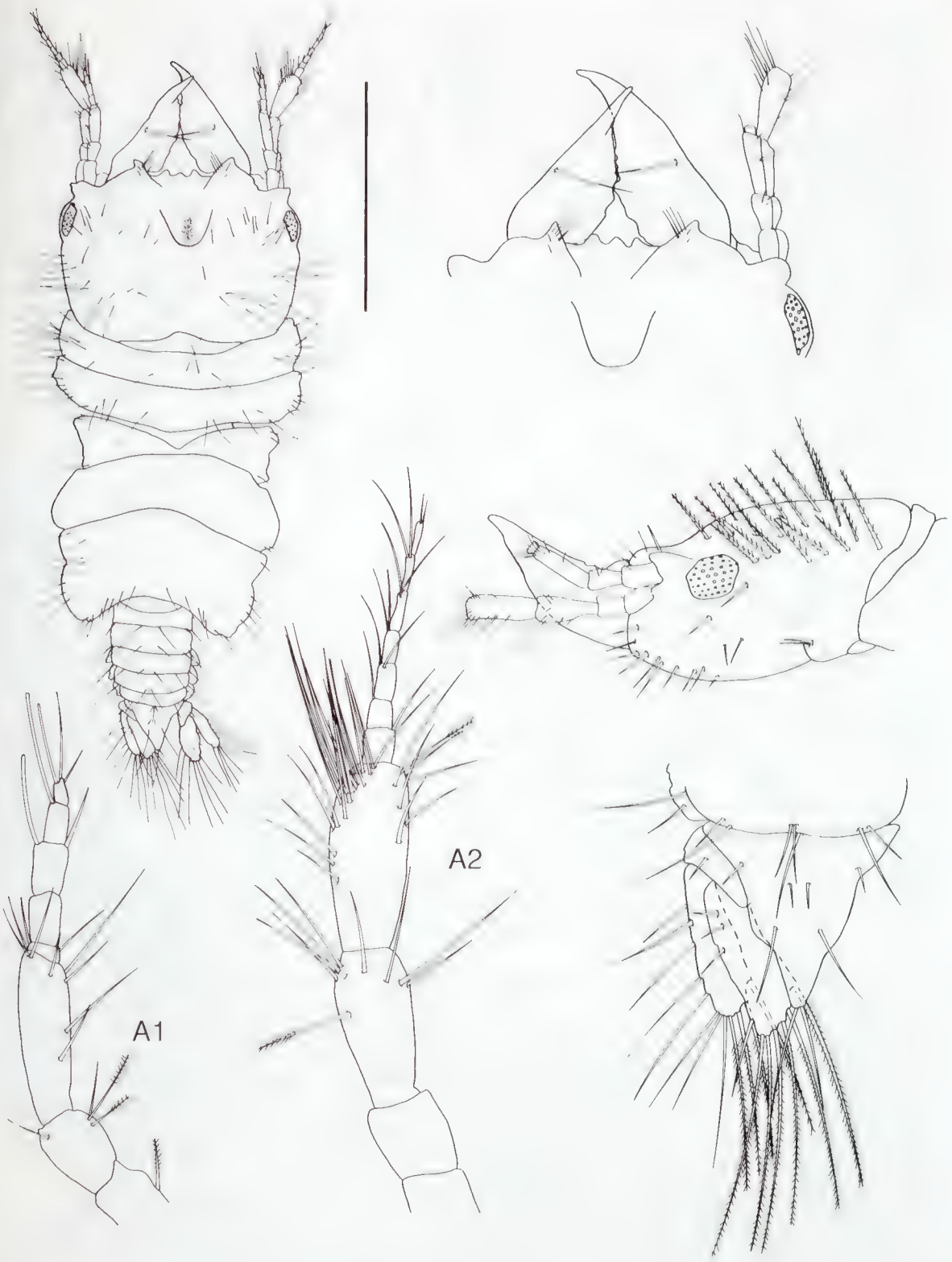


Figure 54. *Gnathia iridomyrmex*. Holotype, NMV J27572.

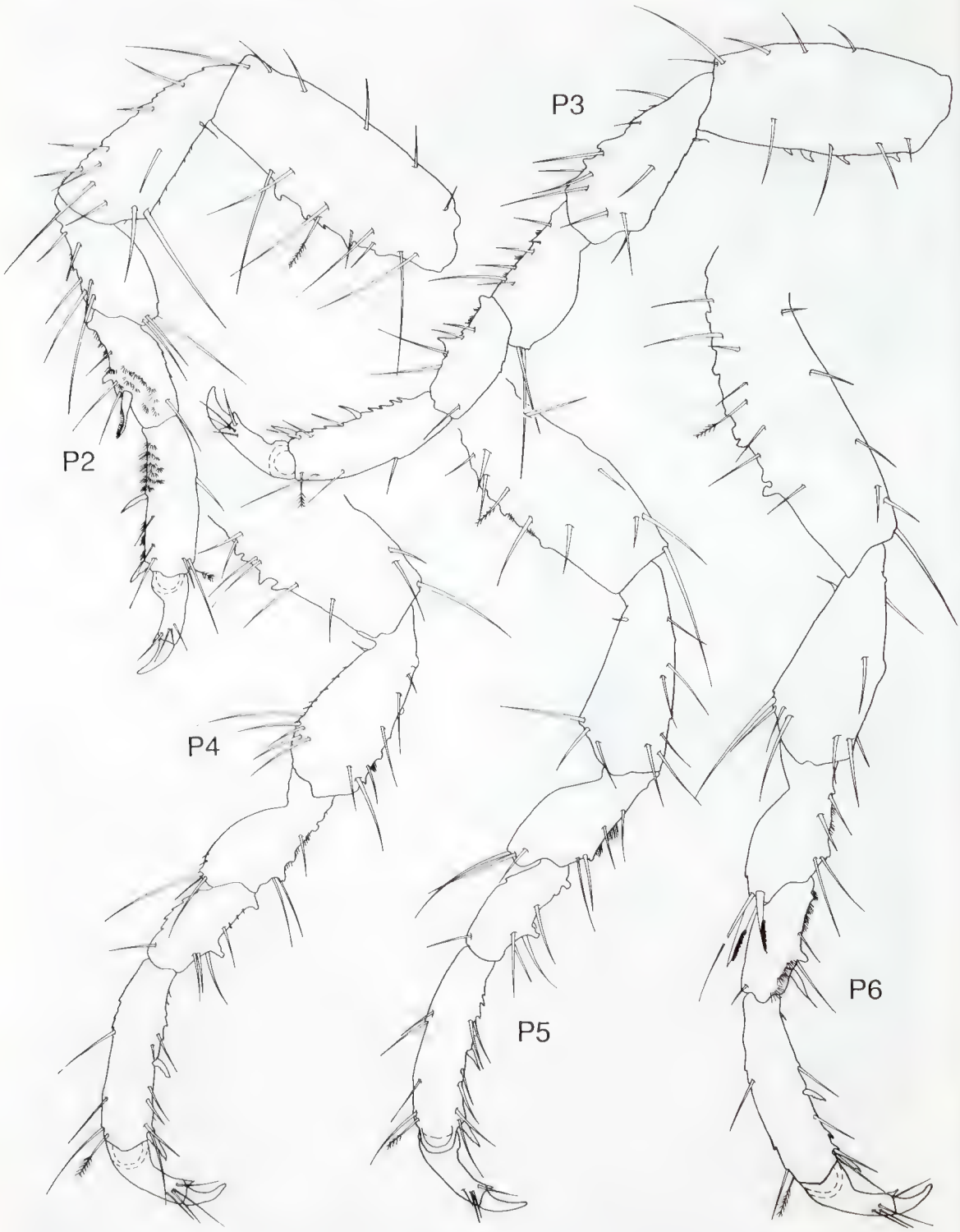


Figure 55. *Gnathia iridomyrmex*. Holotype, NMV J27572.

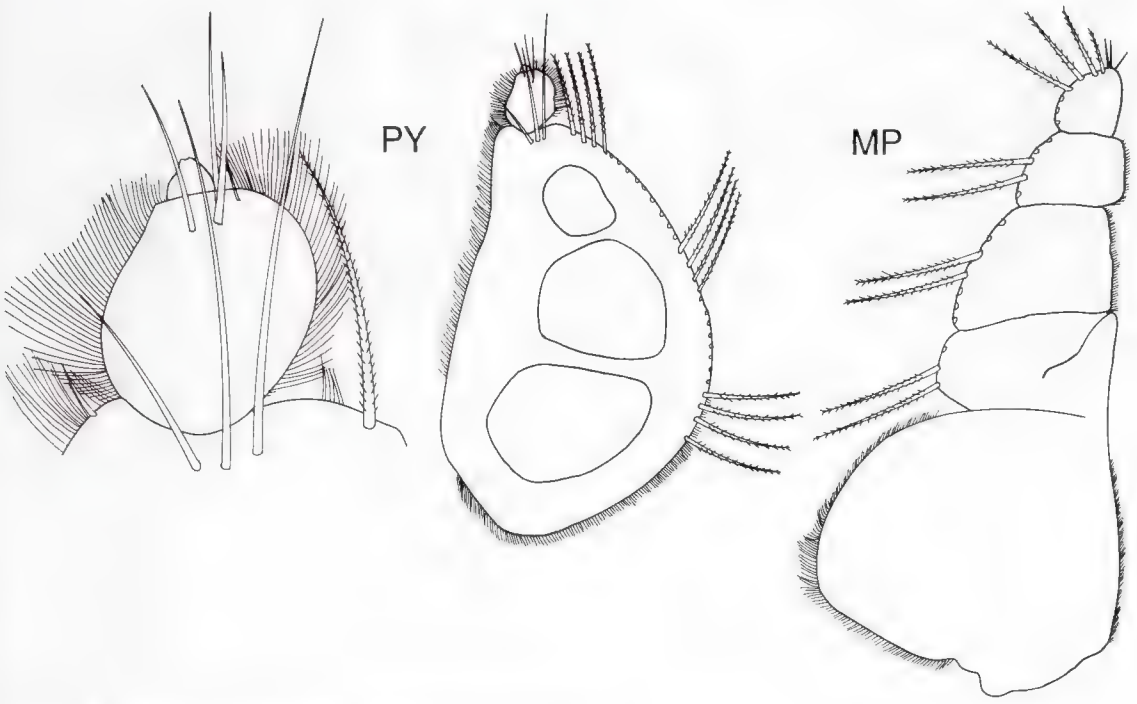


Figure 56. *Gnathia iridomyrmex*. Holotype, NMV J27572.

basis; pereopod 6 with 2 anterior pectinate setae on merus; pereopods 2 and 6 with 1 posterior seta on carpus.

Pleopods setose. Pleopod 2 endopod with appendix masculina half length of rami. Penes 2 small contiguous papillae.

*Distribution.* Western Victoria, rocky substrate, 11 m depth.

*Remarks. Gnathia iridomyrmex* most closely resembles *G. calmani* Monod in the shape of the mediofrontal process, though in *G. iridomyrmex* the mediofrontal process is broader (half the width of the cephalon versus one-third the width). *G. iridomyrmex* also differs in being hirsute; lacking mandibular incisors, the posterior tubercle on the cephalon and anterolateral lobes on pereonite 4. *G. iridomyrmex* is also similar to *G. odontomachus* but differs in possessing a trifid mediofrontal process, more pronounced superior frontolateral processes and a simpler mandibular blade.

### ***Gnathia mystrium*** sp. nov.

Figures 57–59

*Material examined.* Holotype. Tasmania, western Bass Strait, 36 km SSW of Stokes Point, King I. (40°26.7′S, 143°41.4′E), 85 m, medium sand, R.S. Wilson on RV *Tangaroa*, 22 Nov 1981 (stn BSS 198), NMV J27564 (1 male).

Paratypes. All collected by R.S. Wilson on RV *Tangaroa*, Nov 1981. Western Bass Strait, type locality, NMV J8352 (1). 20 km SSW of Stokes Point, King I. (40°19.5′S, 143°48.8′E), 71 m, sandy shell (stn BSS 199), NMV J8351 (1).

Eastern Bass Strait, 25 km NE of Deal I., Tasmania (39°14.8′S, 147°31.5′E), 57 m, medium sand (stn BSS 174), NMV J8353 (1). 100 km NE of North Point, Flinders I. (38°52.6′S, 148°25.2′E), 130 m, fine sand (stn BSS 170), NMV J8354 (1). 37 km NNE of Eddystone Point (40°40.7′S, 148°36.9′E), 67 m, muddy sand (stn BSS 164), NMV J8350 (1).

*Description.* Total length of holotype: 3.07 mm.

Cephalosome quadrate, large, one-third length of animal, lateral margins convex. Eyes well developed, lateral and sessile. Frontal border slightly produced; mediofrontal process inferior, broad with bifid projection; superior frontolateral process conical, with 3 setae on internal margin. Inferior frontolateral process conical, ventral to superior frontolateral process. External scissura very shallow. Supraocular lobe very low, acute. Cephalosome with broad dorsal sulcus; paraocular tubercles and setae; translucent elliptical region anteromedially, above buccal cavity. Antenna 2 longer than

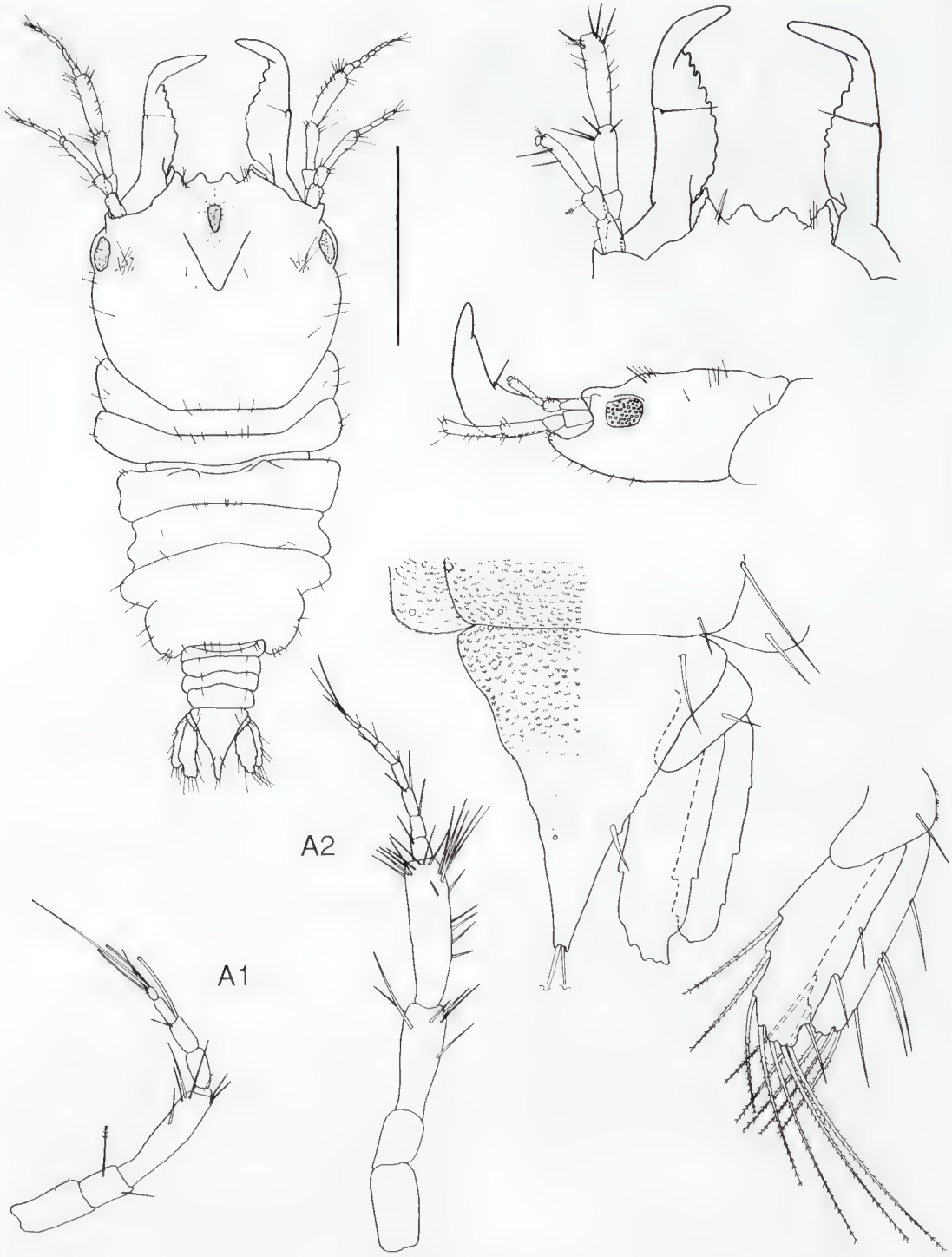


Figure 57. *Gnathia mystrium*. Holotype, NMV J27564.

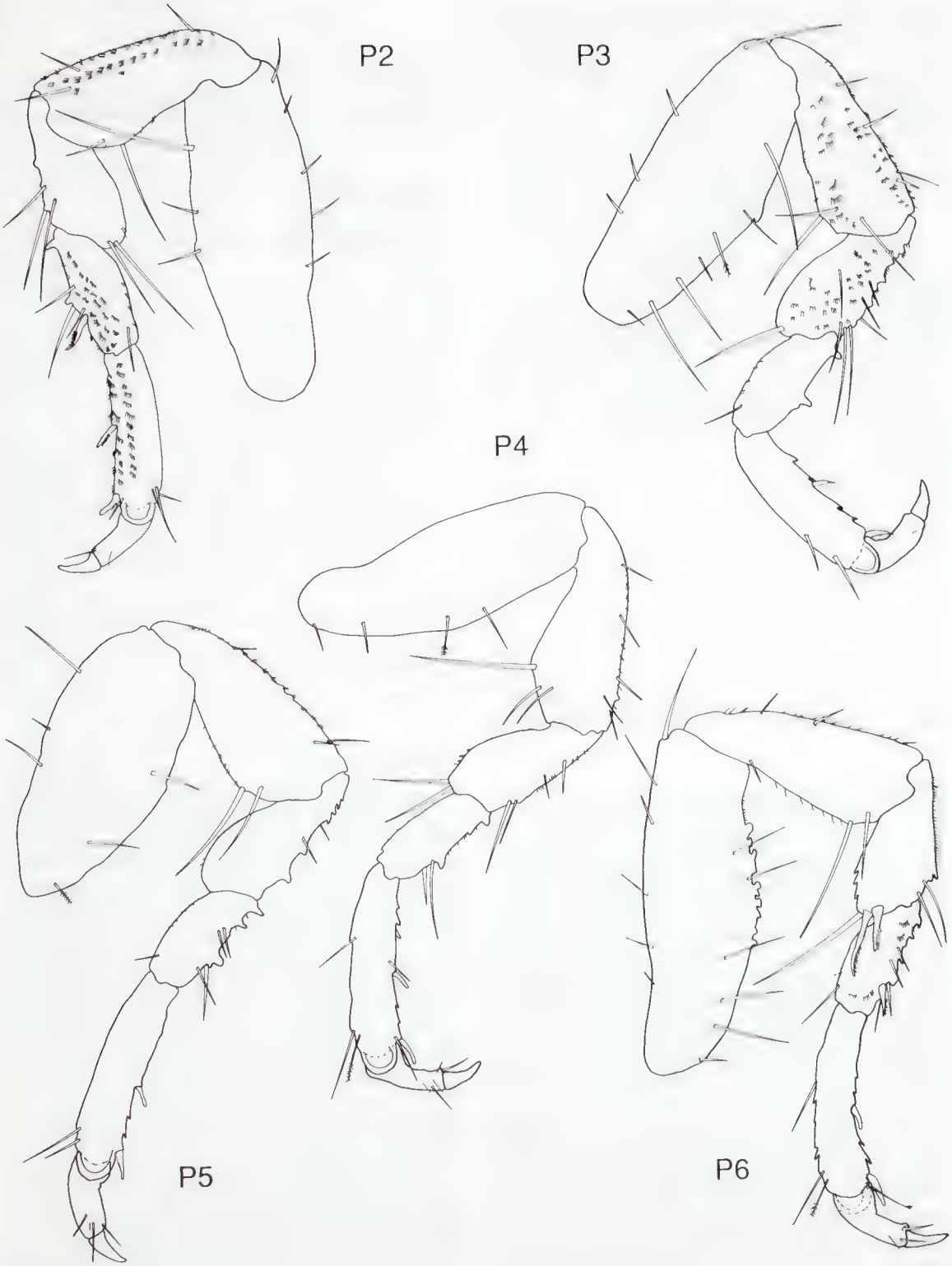


Figure 58. *Gnathia mystrium.* Holotype, NMV J27564.

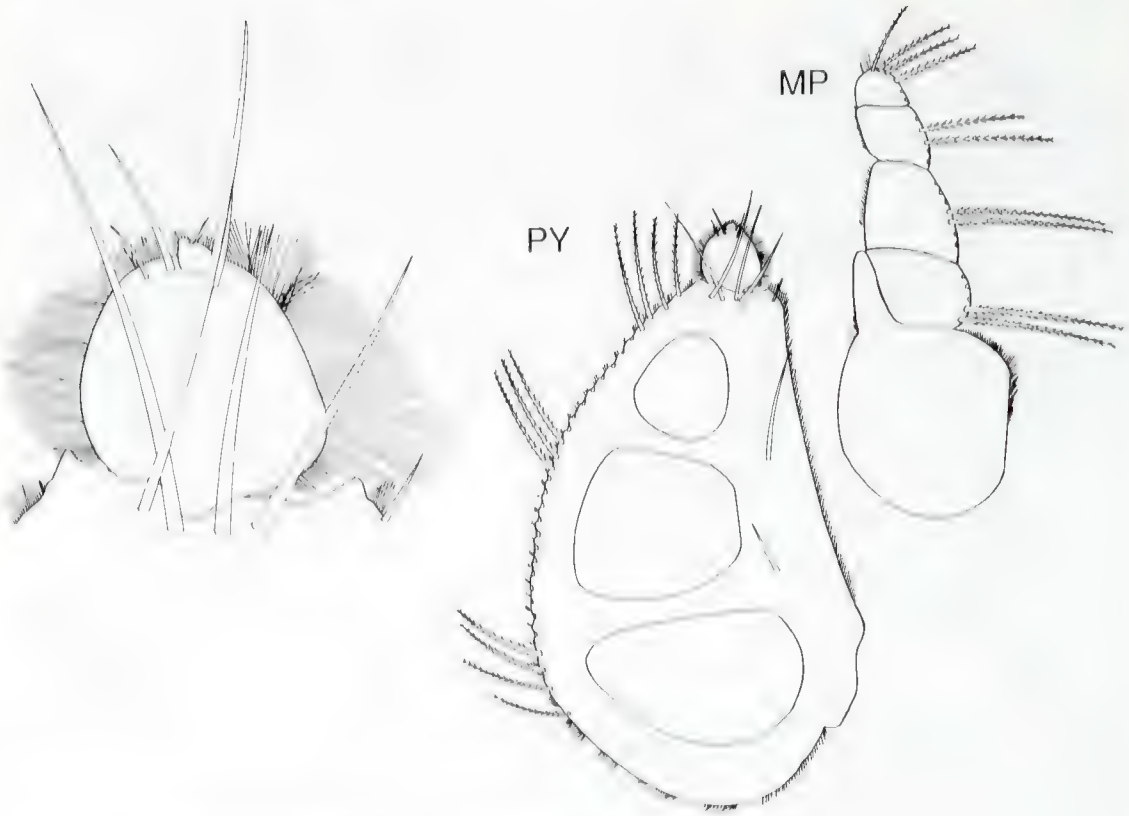


Figure 59. *Gnathia mystrium*. Holotype, NMV J27564.

antenna 1; flagellum of antenna 1 of 5 articles, with 3 aesthetascs; flagellum of antenna 2 of 7 articles. Mandible long, two-thirds length of cephalosome; apex inflexed, distally raised in lateral view at 90°; with unarmed carina; slight mandibular incisor half way along; crenulate blade distally as far as cylindrical apex; seta at midpoint; erisma pronounced. Maxilliped 5-articled; external margins of articles 2–4 bearing plumose setae; endite barely reaching article 3, narrow. Pylopod 3-articled, internal margin of plumose setae; article 1 with 3 areolae and 6 setae on ventral surface, 4 distally; article 2 with 3 setae on ventral surface; article 3 minute.

Pereon widest anteriorly, as wide as cephalosome, margins with numerous setae. Pereonite 1 dorsally fused with cephalosome, not visible. Pereonites 2 and 3 subequal. Pereonite 4 with anterior constriction and 2 anterior lobes. Pereonite 6 long, at least twice as long as other pleonites. Pereonite 7 very narrow, overlapping pleon. Pleon with only 4 segments visible dorsally, other pleonite obscured by pereon; epimera not visible dorsally. Pleotelson subtriangular, longer than wide; lateral margins straight; with 2 pairs of simple setae laterally and pair of setae on distal apex. Uropodal peduncle with 1 seta; rami subequal, reaching apex of pleotelson; rami bearing numerous plumose setae distally.

Pereopods with few simple setae; pereopod 6 with 2 anterior spines on merus and crenulate anterior margin of basis; pereopod 2 and pereopod 6 with posterior spiniform seta on carpus.

Pleopods setose. Pleopod 2 endopod with appendix masculina half length of rami. Penes 2 small contiguous papillae.

*Distribution.* Bass Strait, 57–130 m depth.

*Remarks. Gnathia mystrium* is characterised by a bifid mediofrontal process and the presence of both superior and inferior lateral processes. The cephalosome is very large, one-third the length of the whole animal. The mandibles are long and dorsally inflected and pereonite 1 is indistinguishable.

### *Gnathia notostigma* sp. nov.

Figures 60–62

*Material examined.* Holotype. Victoria, S of Point Hicks (38°14.80′S, 149°9.30′E), 200 m, coarse sand, gravel, WHOI epibenthic sled, M.F. Gomon et al. on ORV *Franklin*, 24 Jul 1986 (stn SLOPE 41), NMV J27574 (1 male).

Paratype. Type locality, NMV J19121 (1 male).

*Description.* Total length of holotype: 4.75 mm.

Cephalosome rectangular, 1.25 times as wide as long, lateral margins convex. Eyes well developed, lateral and sessile. Frontal border produced; mediofrontal process broad with bifid projection, with 3–4 setae laterally in indentation between processes; superior frontolateral process conical, with 4 setae spread evenly along external margin. Mediofrontal process paler than rest of frontal border in some specimens, appearing to be located ventral to superior frontolateral process but no sutures were found between processes. External scissura rounded. Supraocular lobe very low, acute. Cephalosome with short dorsal sulcus; very pronounced paraocular tubercles forming slight mesolateral ridge, ornamentation particularly noticeable in lateral view. Antenna 2 longer than antenna 1; flagellum of antenna 1 of 5 articles, without aesthetases; flagellum of antenna 2 of 7 articles. Mandible straight, two-thirds length of cephalosome; with unarmed carina; slight mandibular incisor half-way along; ventral dentate blade on distal half, with smooth pseudoblade dorsally; internal lobe on proximal half a long crenulate lamina; seta at midpoint; crisma pronounced. Maxilliped 5-articled; external margins of articles 2–4 bearing plumose setae; endite short, narrow. Pylopod 3-articled, internal margin of simple setae; article 1 with 3 areolae along internal margin, with 12 setae distally on ventral surface and along internal margin, article 2 with 6 setae on ventral surface; article 3 minute.

Pereon evenly sided, as wide as cephalosome. Pereonite 1 dorsally small, not reaching lateral margins and partially obscured laterally by pereonite 2. Pereonites 2 and 3 subequal. Pereonite 4 with anterior constriction. Pereonites 5 and 6 together longer than rest combined. Pereonite 7 very narrow, overlapping pleon. Pleonites 1-4 subequal, 5 narrower; pleonal epimera prominent. Pleotelson subtriangular, longer than wide; lateral margins sinuous, slightly notched distally; with 2 pairs of simple setae and pair of setae on distal apex. Uropodal peduncle with 1 seta; rami subequal, reaching apex of pleotelson, bearing numerous plumose setae distally.

Pereopods with a moderate cover of simple setae; pereopod 6 with 2 anterior spiniform setae on merus; pereopod 2 with 1 posterior spiniform seta on carpus; pereopods 2, 5 and 6 with crenulate anterior margin of basis.

Pleopods setose. Pleopod 2 endopod with appendix masculina half length of rami. Penes 2 small contiguous papillae.

*Distribution.* Eastern Bass Strait, 200 m depth.

*Remarks. Gnathia notostigma* is differentiated from other Australian species by the very pronounced paraocular ornamentation and ridge most clearly seen in lateral view. *G. lignophila* Müller from Malaysia also has similar paraocular ornamentation and both species possess a narrow maxilliped endite. *G. notostigma* differs from *G. lignophila* in possessing shorter and more robust mandibles with a pseudoblade; a conical mediofrontal process with notched lateral margins and only a slight median depression while the mediofrontal process of *G. lignophila* is bifid (large median depression) with smooth lateral margins; and *G. lignophila* unlike *G. notostigma*, is densely covered in granules anteriorly. *G. notostigma* is also similar to *G. camponotus* but differs in possessing a more pronounced and anterior paraocular ornamentation and a mediofrontal process with a slight median notch.

### *Gnathia odontomachus* sp. nov.

Figures 63–65

*Material examined.* Holotype. Victoria, Western Port, off Crib Point (38°20.94′S, 145°13.33′E), 8 m, fine sand mud, Smith-McIntyre grab, A.J. Gilmour, Marine Studies Group on FV *Melita*, 29 Mar 1965 (stn CPBS-N 21), NMV J4374 (1 male).

Paratypes. Western Port, off Crib Point (38°20.81′S, 145°13.85′E), 13 m, gravel sand, Smith-McIntyre grab, A.J. Gilmour, Marine Studies Group on FV *Melita*, 30 Mar 1965 (stn CPBS-N 41), NMV J4370 (1 male); 10 m, 10 Mar 1965 (stn CPBS-N 23), NMV J4372 (1 male).

*Description.* Total length of holotype: 2.95 mm.

Cephalosome rectangular, 1.33 times as wide as long, lateral margins slightly convex. Eyes well developed, lateral and sessile. Frontal border transverse; mediofrontal process inferior, small, conical; superior frontolateral process rounded, with 3 large setae clumped on internal margin and 3 smaller setae evenly spaced on

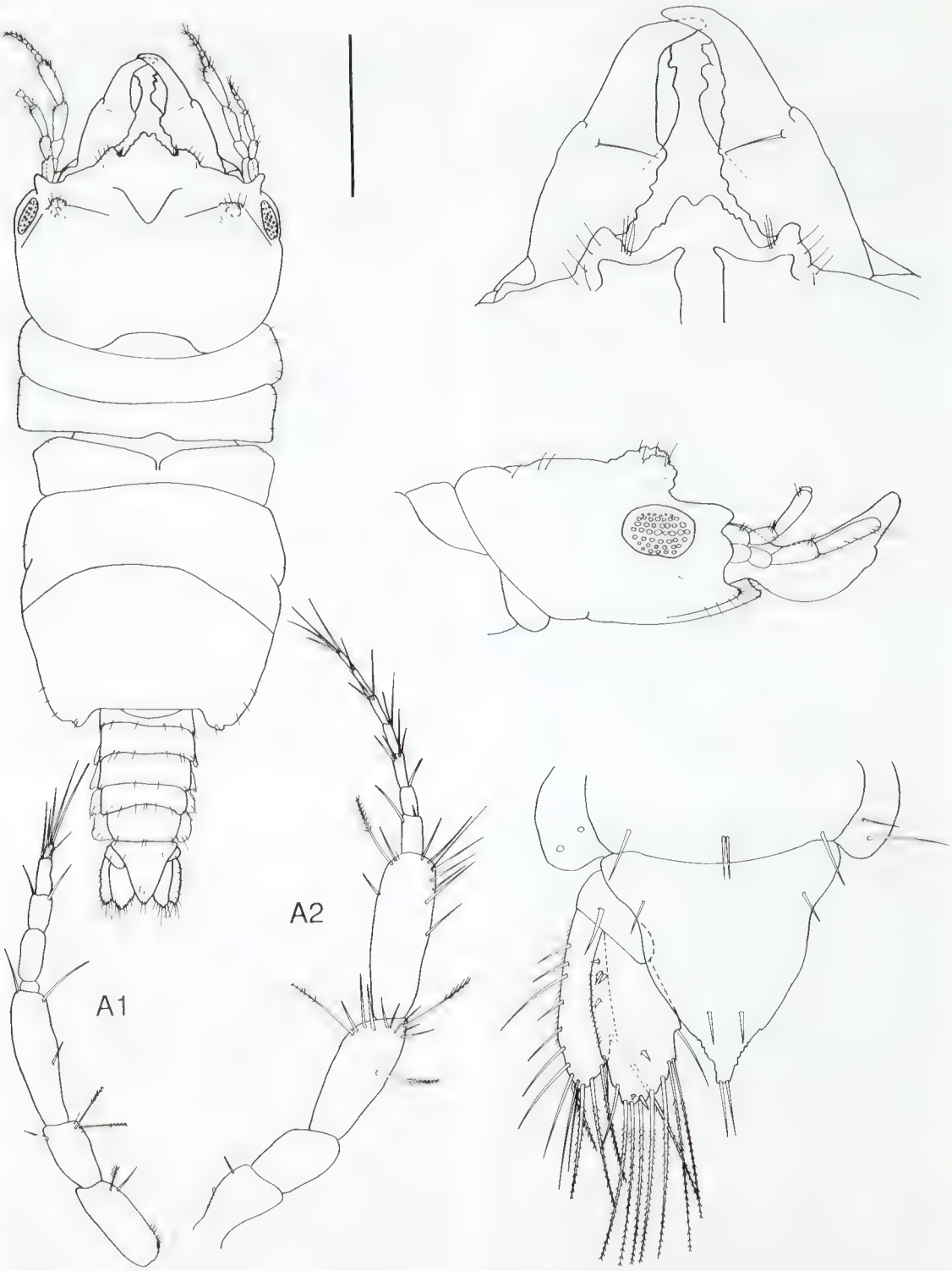


Figure 60. *Gnathia notostigma*. Holotype, NMV J27574.

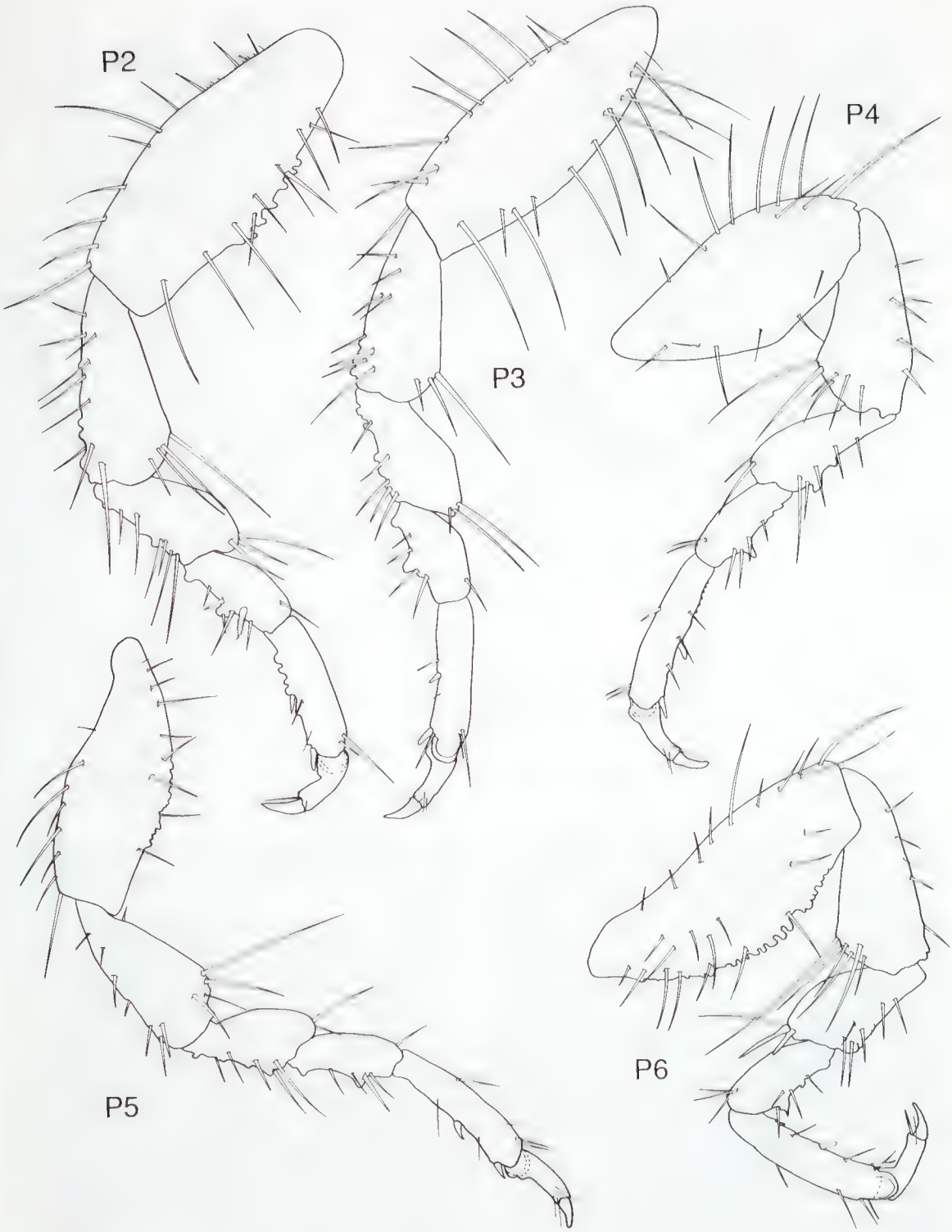


Figure 61. *Gnathia notostigma*. Holotype, NMV J27574.

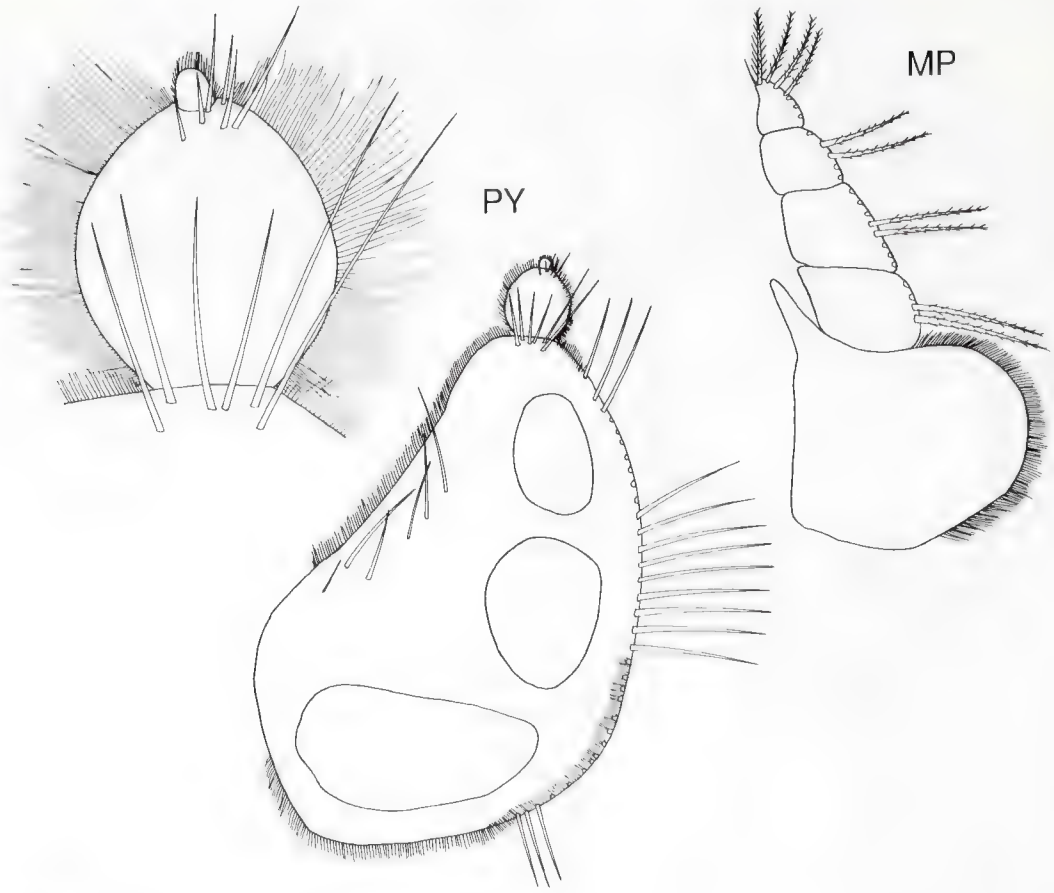


Figure 62. *Gnathia notostigma*. Holotype, NMV J27574.

external margin. External scissura very shallow. Supraocular lobe not pronounced. Cephalosome with small dorsal sulcus and translucent, elliptical region anteromedially, within sulcus and above buccal cavity. Antenna 2 twice as long as antenna 1; flagellum of antenna 1 of 5 articles, with 2 aesthetascs, peduncle length subequal to flagellum; flagellum of antenna 2 of 7 articles. Mandible straight, two-thirds length of cephalosome; proximal third a pronounced basal neck; middle third progressively narrower, ventral dentate blade; distal third a long, cylindrical apex; with unarmed carina; mandibular incisor half-way along; seta at midpoint near incisor; erisma pronounced. Maxilliped 5-articled; external margins of articles 2–4 bearing plumose endite barely reaching article 3, narrow. Pylopod 3-articled, internal margin of plumose setae; article 1 with ring of short, stouter setae posteriorly, with 3 areolae distally and 12 setae distally on ventral surface and along median margin; article 2 with 7 setae on ventral surface; article 3 minute.

Pereon evenly sided, as wide as cephalosome, covered with numerous simple setae. Pereonite 1 dorsally reaching lateral margins, partially obscured laterally by pereonite 2; pereonite 4 with a slight anterior constriction and wide median groove; pereonite 5 with areae laterales. Pereonite 7 very narrow, overlapping pleon. Pleonites progressively narrower, pleonal epimera prominent. Pleotelson subtriangular, as wide as long, with few tubercules; lateral margins slightly sinuous; with 3 pairs of simple setae and pair of setae on distal apex. Uropodal peduncle with 1 seta; endopod longer than exopod, reaching apex of pleotelson; rami bearing numerous plumose setae distally.

Pereopods subequal, with moderate cover of simple setae; pereopod 2 with 1 posterior pecti-

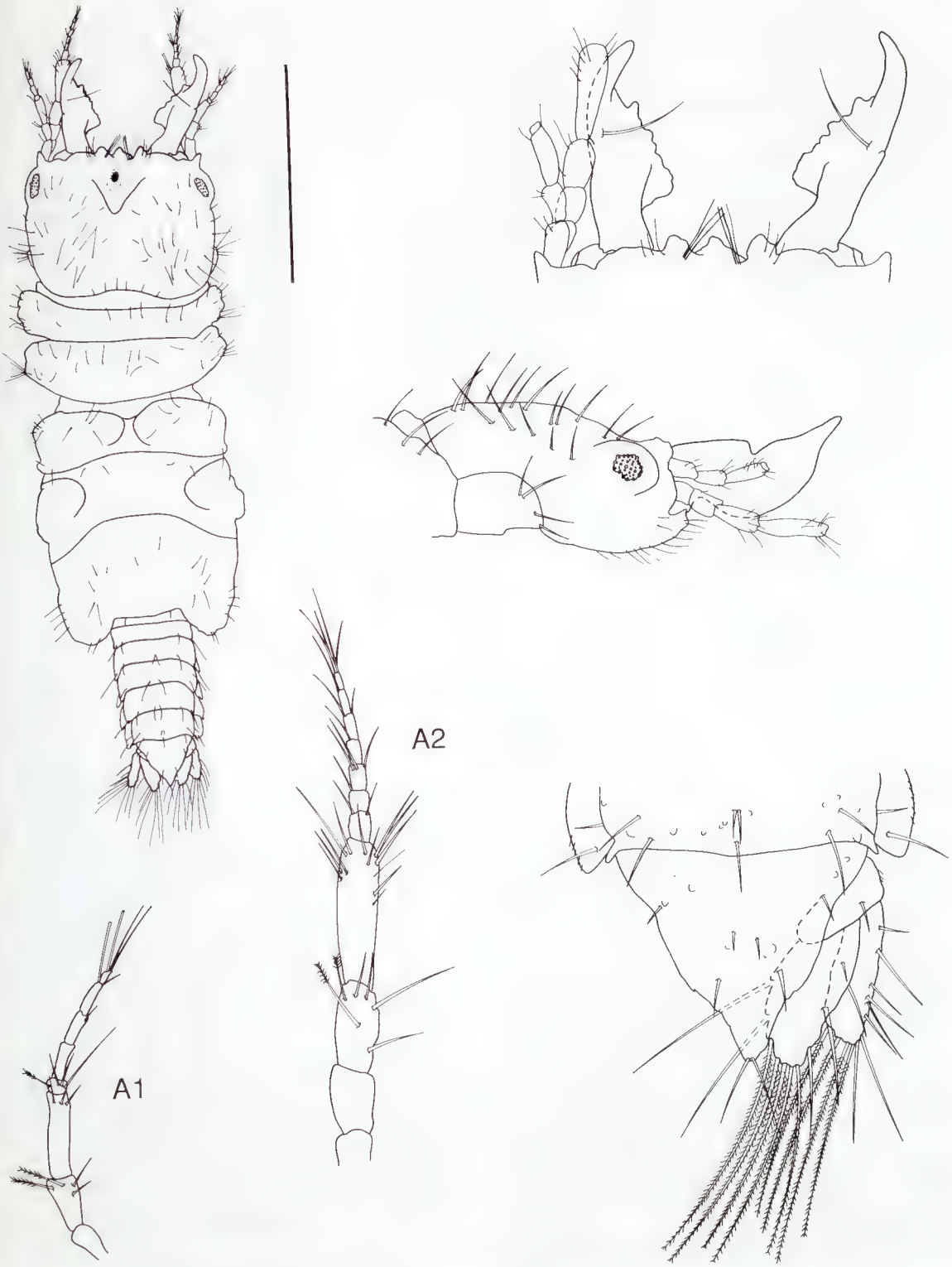


Figure 63. *Gnathia odontomachus*. Holotype, NMV J4374.

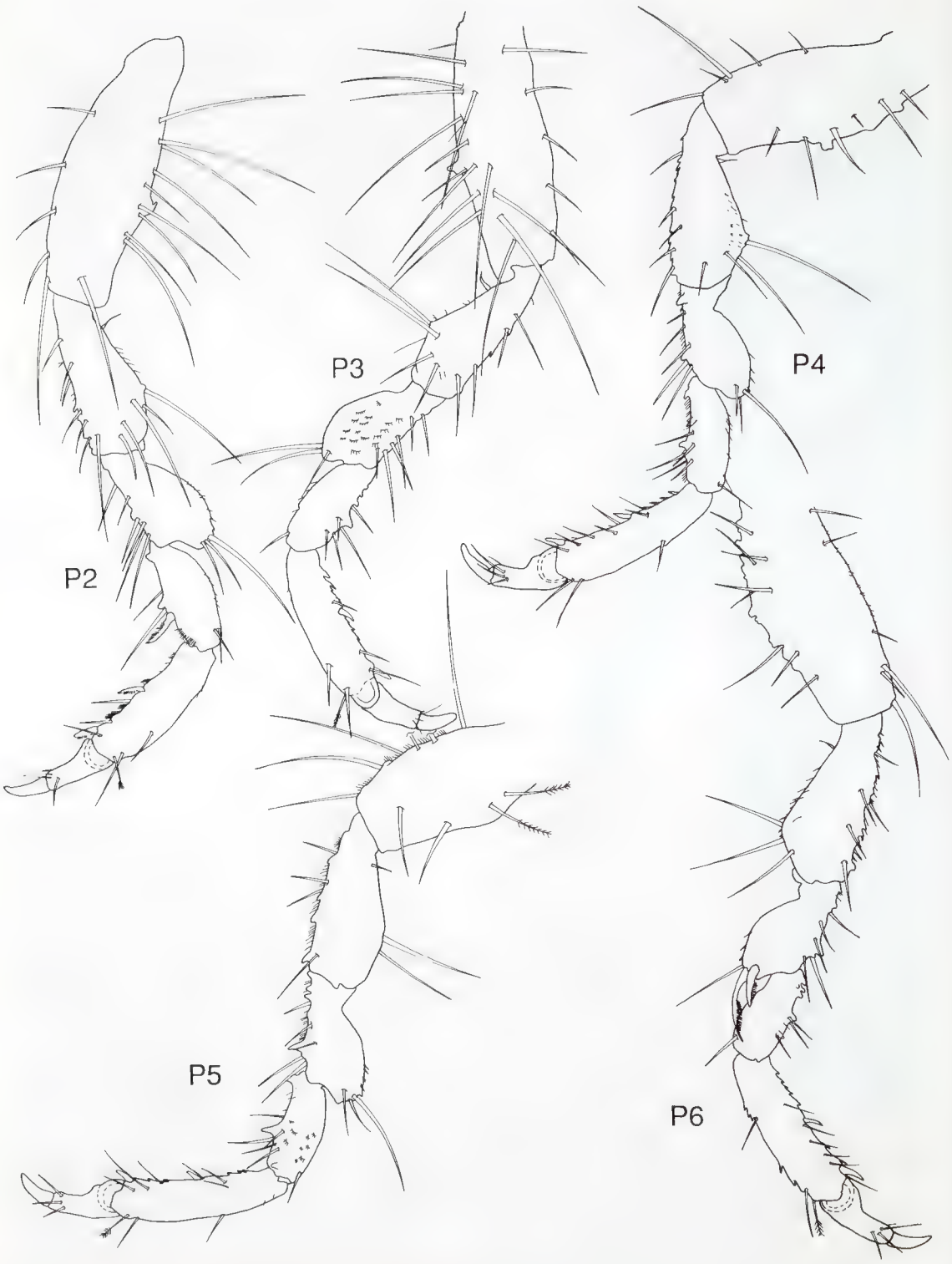


Figure 64. *Gnathia odontomachus*. Holotype, NMV J4374.

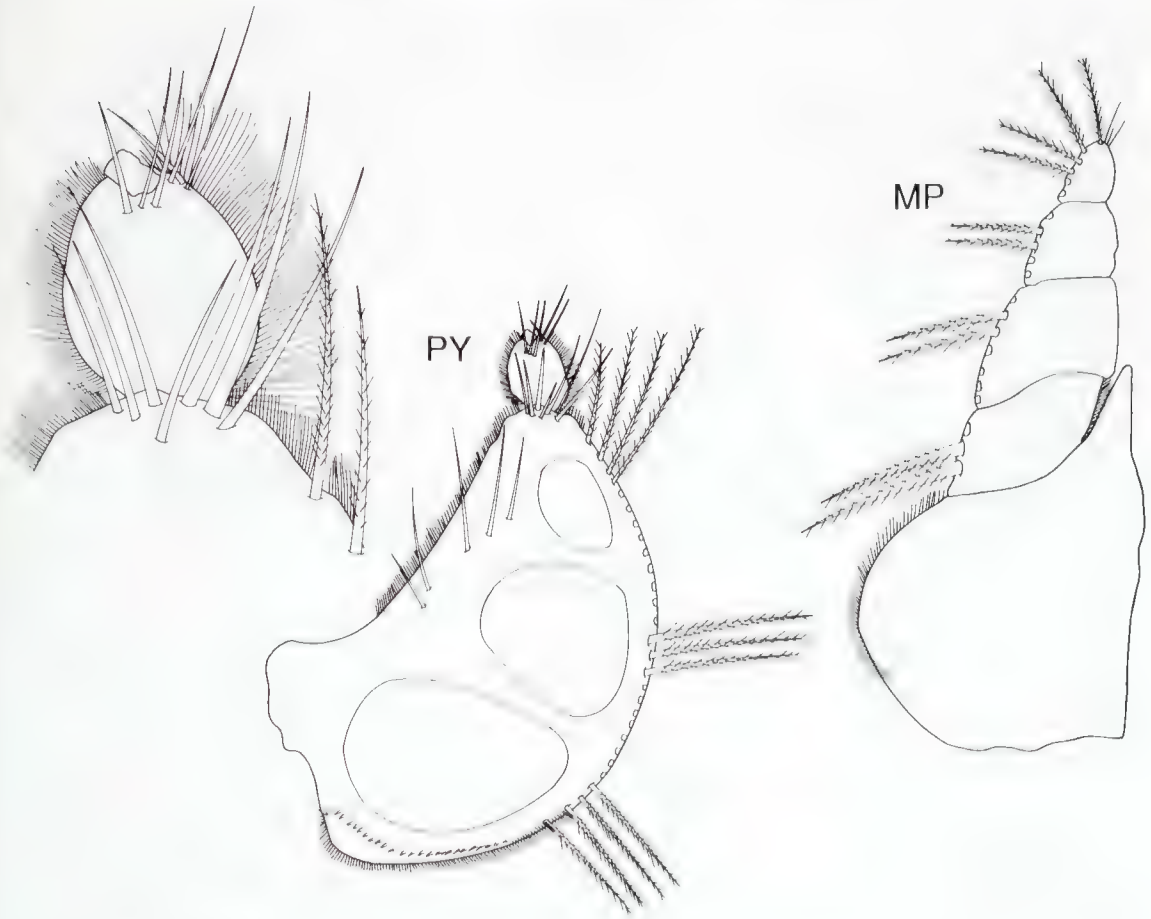


Figure 65. *Gnathia odontomachus*. Holotype, NMV J4374.

nate seta on carpus; pereopod 6 with 2 anterior pectinate setae on merus and crenulate anterior margin of basis.

Pleopods setose. Pleopod 2 endopod with appendix masculina half length of rami. Penes 2 small contiguous papillae.

*Distribution* Off Crib Point, Western Port, Victoria, 8–13 m depth.

*Remarks. G. odontomachus* is one of many species from around the world which possess a inferior, conical medifrontal process and conical superior processes. Of the Australian fauna it most closely resembles *G. latidens* (Beddard) though is easily disinguished by its hirsute nature; more rounded mediofrontal process; and the lack of a pseudoblade.

***Gnathia prolasius*** sp. nov.

Figures 66–68

*Material examined.* Holotype. Victoia, S of Point Hicks (38°21.90′S, 149°20.00′E), 1000 m, WHOI epibenthic sled, G.C.B. Poore et al. on ORV *Franklin*, 23 Jul 1986 (stn SLOPE 32), NMV J27577 (1 male).

Paratypes. All collected with WHOI epibenthic sled by G.C.B. Poore et al. on ORV *Franklin*, Jul 1986. Tasmania, off Freycinet Peninsula (42°0.20′S, 148°37.70′E), 720 m, coarse shelly sand (stn SLOPE 46), NMV J19111 (1 male). 42°2.20′S, 148°38.70′E, 800 m, coarse shelly sand, (stn SLOPE 45), NMV J19113 (1 male).

Victoria, S of Point Hicks (38°21.90′S, 149°20.00′E), 1000 m (stn SLOPE 32), NMV J27573 (20 males). 38°16.40′S, 149°27.60′E, 800 m, coarse shell (stn SLOPE 34), NMV J19112 (2 males).

Other material. New South Wales, off Eden (37°0.60′S, 150°20.70′E), 363 m, coarse shell (stn SLOPE 22), NMV J19114 (34).

Victoria, S of Point Hicks (38°21.90′S, 149°20.00′E), 1000 m (stn SLOPE 32), NMV J19115 (500).

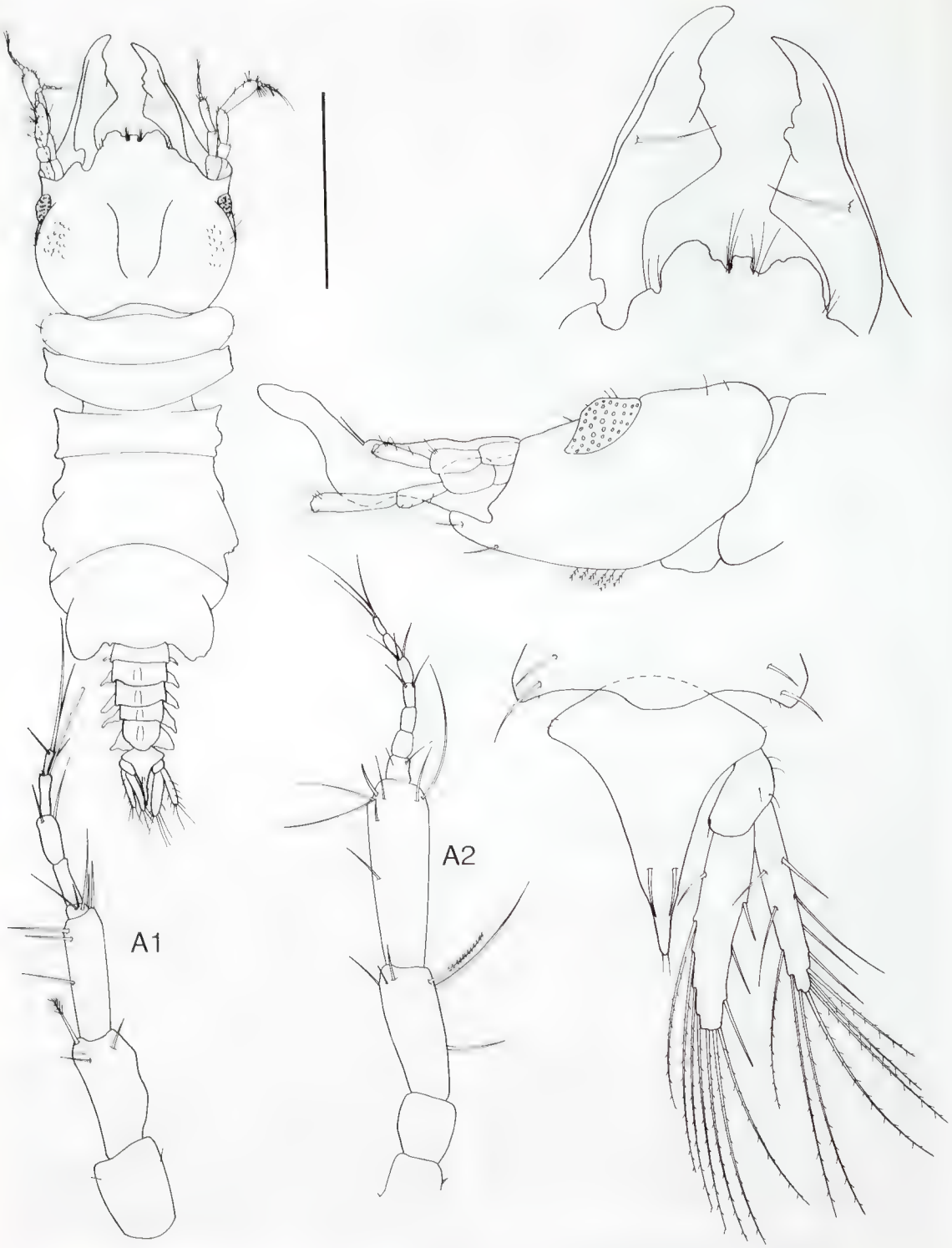


Figure 66. *Gnathia prolasius*. Holotype, NMV J27577.

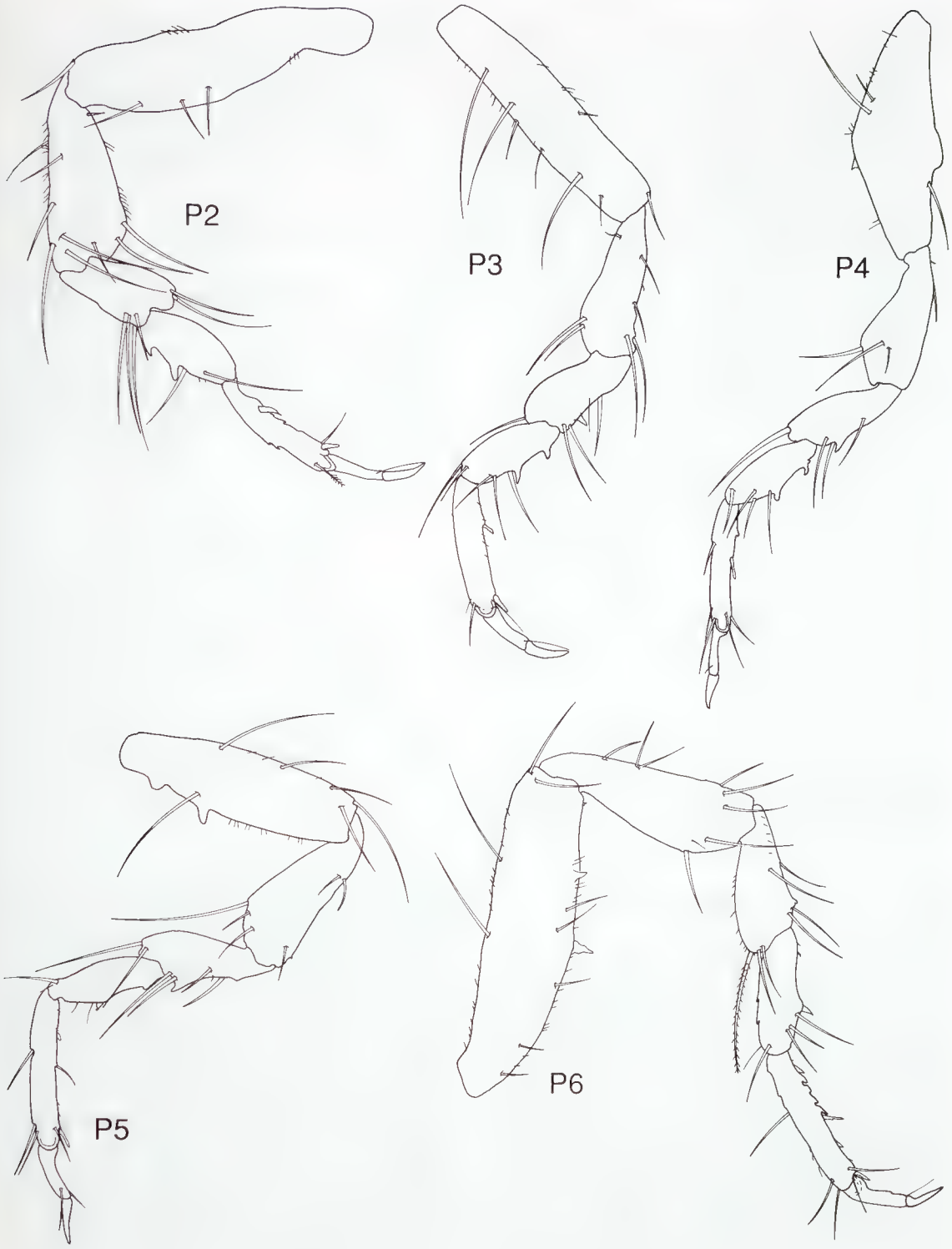


Figure 67. *Gnathia prolasius*. Holotype, NMV J27577.

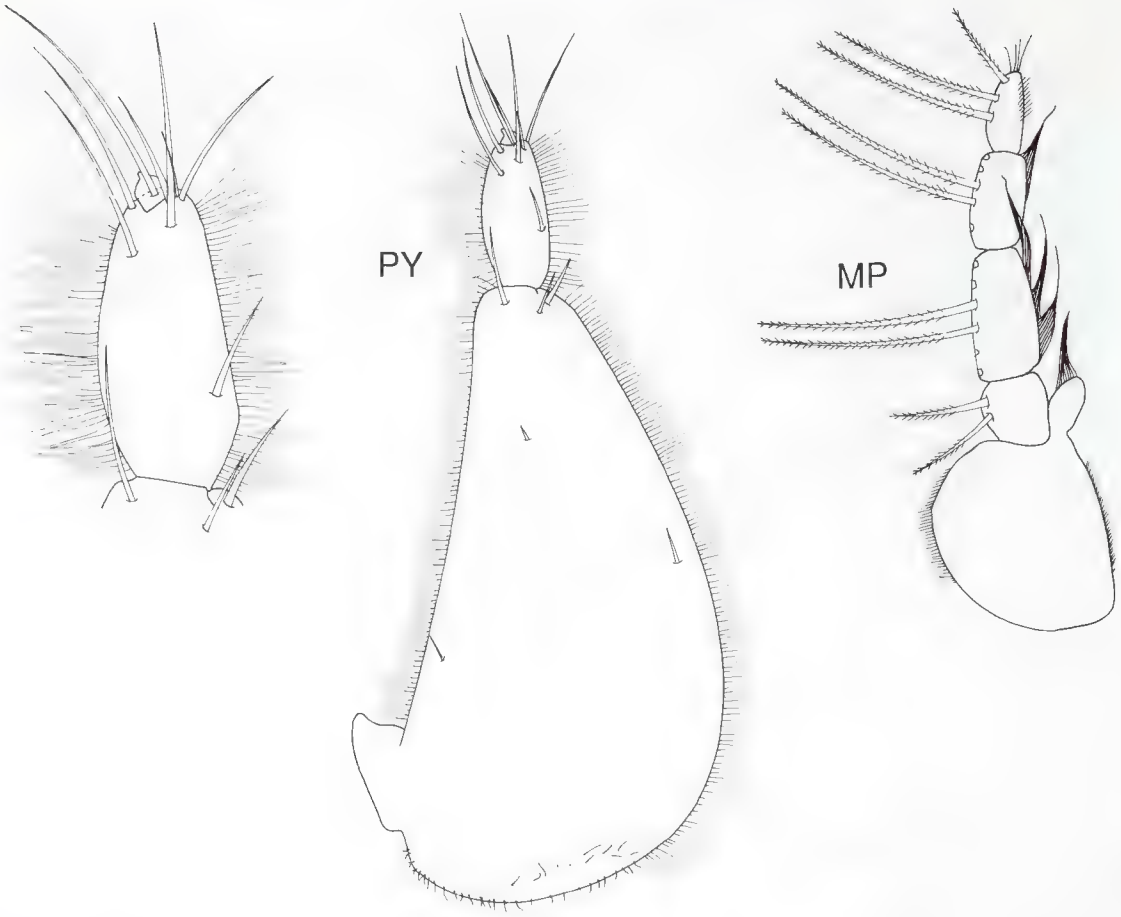


Figure 68. *Gnathia prolasius*. Holotype, NMV J27577.

*Description*. Total length of holotype: 3.49 mm.

Cephalosome rectangular, 1.2 times as wide as long, lateral margins convex. Eyes well developed, lateral and sessile. Frontal border produced; mediofrontal process quadrate, with 4 setae laterally; superior frontolateral process large, rounded, with anteromedial notch, twice length of mediofrontal process, with 2 small setae laterally. External scissura smoothly rounded. Supraocular lobe very low, acute. Cephalosome with broad dorsal sulcus; paraocular granules posterior to eye. Antenna 2 longer than antenna 1; flagellum of antenna 1 of 5 articles, with 1 aesthetasc; flagellum of antenna 2 of 7 articles. Mandible straight, raised distally; two-thirds length of cephalosome; with unarmed carina; blade complex, crenulate distally while smooth and linear proximally; seta at midpoint; basal neck smoothly arced; erisma pronounced, external lateral margin flattened. Maxilliped 5-articled, palp thin and elongate; external margins of articles 2–4 bearing plumose setae; internal margin with long setae joined together into 5 strands; endite short, narrow. Pylopod 3-articled, elongate and narrow, internal margin of fine short setae; with ring of short, stouter setae posteriorly; article 1 with 6 setae on ventral surface; article 2 elongate, with 7 setae distally on ventral surface; article 3 minute.

Pereon evenly sided, as wide as cephalosome. Pereonite 1 barely reaching lateral margins dorsally and partially obscured laterally by pereonite 2. Pereonites 2 and 3 subequal; pereonite 4 rectangular, longer than 2 and 3, with anterior constriction. Pereonite 5 and 6 rounded, as long as others together. Pleonites progressively narrower, pleonal epimera prominent. Pleotelson

subtriangular, longer than wide; lateral margins slightly concave; with pair of simple setae and pair of setae on distal apex. Uropodal peduncle with 5 small setae; endopod longer than exopod, reaching beyond apex of pleotelson.

Pereopods narrow, with few simple setae; ischium to carpus with small lateral projections.

Pleopods without setae. Pleopod 2 endopod lacking appendix masculina. Penes 2 small contiguous papillae.

*Distribution.* Eastern Bass Strait and south-eastern slope, 363–1000 m depth.

*Remarks. Gnathia prolasius* is similar to *G. stigmacros* in overall body proportions, particularly the pereopods and mouthparts. *G. prolasius* is easily recognised by the large, semicircular frontolateral processes.

### ***Gnathia rhytidoponera*** sp. nov.

Figures 69–71

*Material examined.* Holotype. Western Coral Sea, NE of Townsville, Queensland (17°57′S, 147°02′E), 287–300 m, epibenthic sledge, M. Pichon et al. on RV *Cidaris*, 16 Jun 1986 (stn 146.2), QM W19962 (1 male).

Paratype. Western Coral Sea, NE of Townsville, Queensland (17°22′S, 146°48′E), 303–296 m, epibenthic sledge, M. Pichon et al. on RV *Cidaris*, 15 Jun 1986 (stn 143.2), QM W19963 (1 male)

*Description.* Total length of holotype: 3.86 mm.

Cephalosome subquadrate with a pronounced ventral rostrum, lateral margins convex. Rostrum narrow, conical with small lateral indentations. External scissura smoothly rounded. Cephalosome with a narrow dorsal sulcus extending medianly, all the way to frontal border. Antenna 2 two times longer than antenna 1; flagellum of antenna 1 of 5 articles with 3 aesthetases; flagellum of antenna 2 of 7 articles, peduncle articles 3 and 4 with numerous small setae. Mandible straight, two-thirds length of cephalosome; with unarmed carina; seta at midpoint; smooth ventral blade on proximal two-thirds, visible in lateral view, with a dentate pseudoblade dorsally; a quadrate internal lobe on proximal dorsal surface of mandible, clearly visible in lateral view. Maxilliped 5-articled; external margins of articles 2–4 bearing plumose setae; endite barely reaching article 3. Pylopod 3-articled, internal margin of plumose setae; article 1 with 3 large areolae and 7 setae on ventral surface, 4 distally; article 2 with 4 setae distally on ventral surface; article 3 minute.

Pereon widest anteriorly, as wide as cephalosome. Pereonite 1 weakly fused with cephalosome, barely reaching lateral margins dorsally and partially obscured laterally by pereonite 2. Pereonites 2 and 3 subequal; pereonite 4 narrower than others, with anterior constriction; pereonites 5 and 6 together longer than others together. Pereonite 6 with small lobuii. Pereonite 7 very narrow, overlapping pleon. Pleon widest in middle; pleonites 3–5 with prominent epimera. Pleotelson subtriangular, longer than wide; lateral margins sinuous; with 1 pair of simple setae medianly and pair of setae on distal apex. Uropodal peduncle with 2 setae; rami subequal, reaching apex of pleotelson; internal margins of rami bearing numerous plumose setae.

Pereopods subequal, with few long simple setae. Pereopod 6 with 2 anterior pectinate setae on merus; pereopods 2 and 6 with posterior spiniform seta on carpus.

Pleopods setose. Pleopod 2 endopod with appendix masculina subequal length to rami. Penes 2 small contiguous papillae.

*Distribution.* Western Coral Sea, NE of Townsville, Queensland, 287–303 m depth.

*Remarks. Gnathia rhytidoponera* is very similar to *G. halei* Cals from southern Queensland. *G. rhytidoponera* differs in possessing a dorsally directed quadrate lobe on the posterior mandibles and lacking a row of setae each side of the base of the mediofrontal process.

### ***Gnathia stigmacros*** sp. nov.

Figures 72–74

*Material examined.* Holotype. Victoria, S of Point Hicks (38°14.80′S, 149°9.30′E), 200 m, coarse sand, gravel, WHOI epibenthic sled, M.F. Gomon et al. on ORV *Franklin*, 24 Jul 1986 (stn SLOPE 41), NMV J27576 (1 male).

Paratypes. Type locality, NMV J19122 (22 males).

Other material. Tasmania, eastern Bass Strait, 82 km ENE of North Point, Flinders I. (39°27.7′S, 148°41.4′E), 293 m, coarse sand, naturalists' dredge, G.C.B. Poore on HMAS *Kimbla*, 28 Mar 1979 (stn BSS 36), NMV J7793 (8); 70 km ENE of North Point, Flinders I. (39°28.4′S, 148°41.8′E), 110 m, coarse sand (stn BSS 35), NMV J7794 (2); 50 km NE of Babel I. (39°40.3′S, 148°46.5′E), 293 m, rock, coarse sand (stn BSS 33), NMV J7795 (11).

Victoria, eastern Bass Strait, near Pt Ricardo (37°53′S, 148°30′E), 27–45 m, medium sand, Smith-

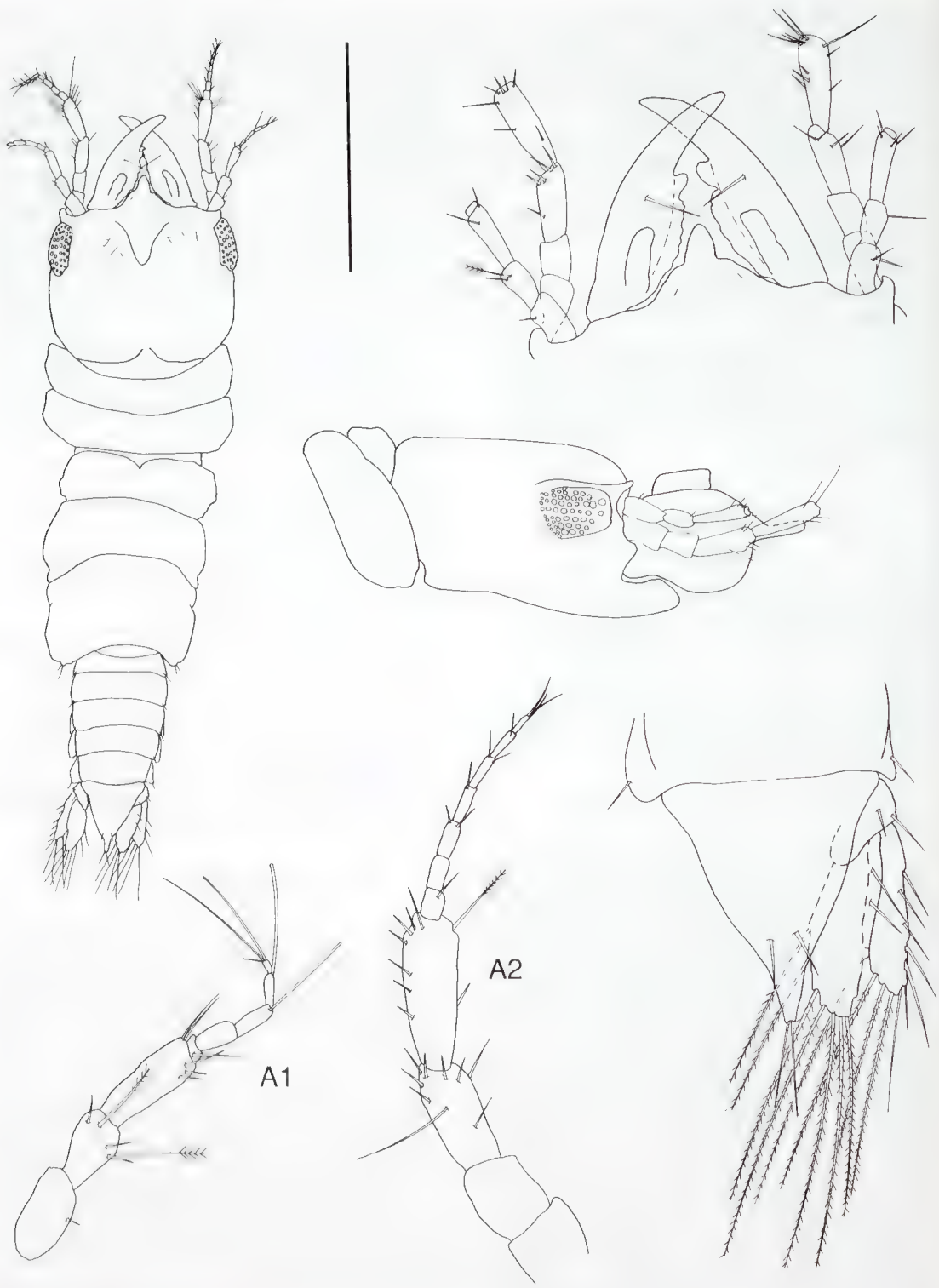


Figure 69. *Gnathia rhytidoponera*. Holotype, QM W19962

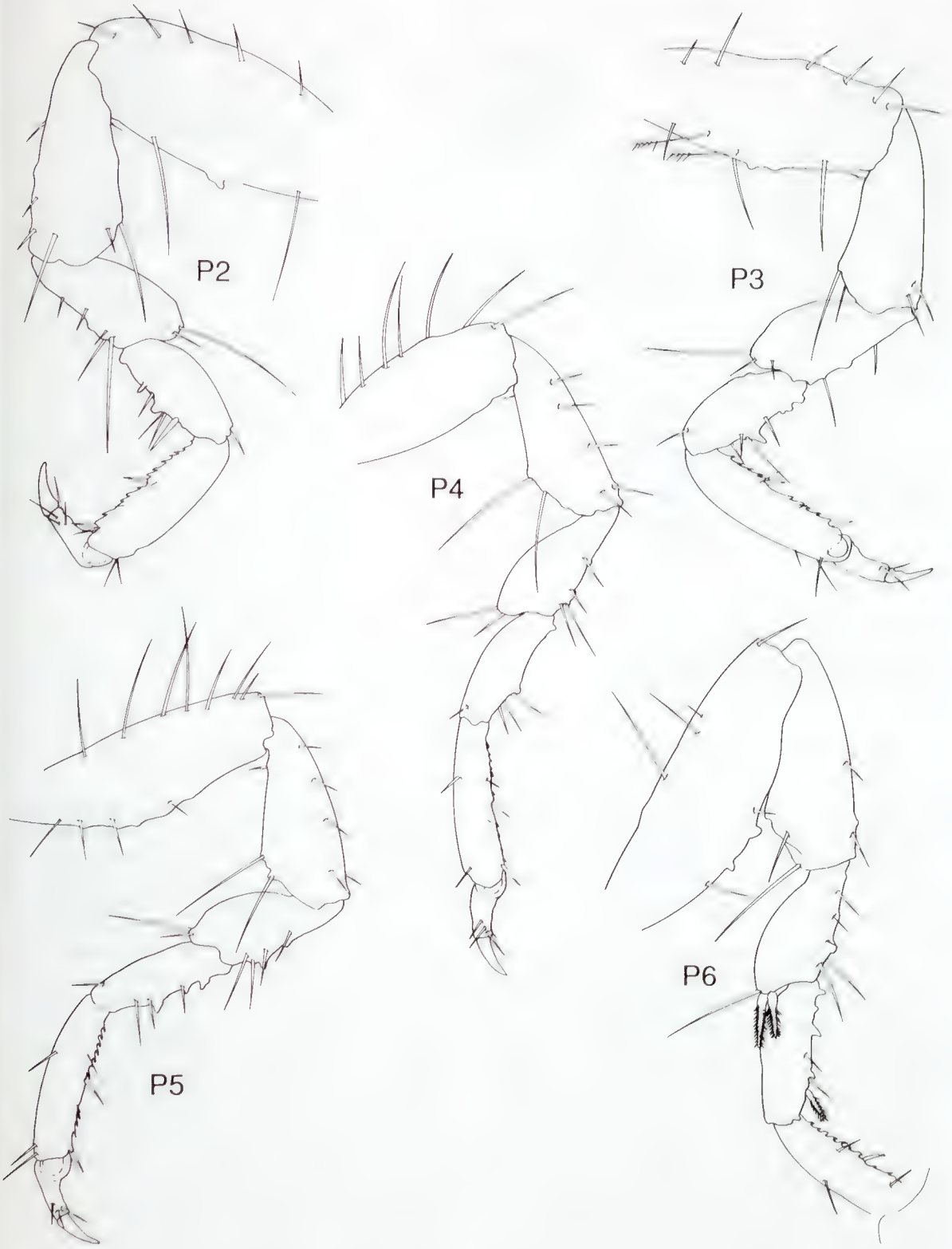


Figure 70. *Gnathia rhytidoponera*. Holotype, QM W19962

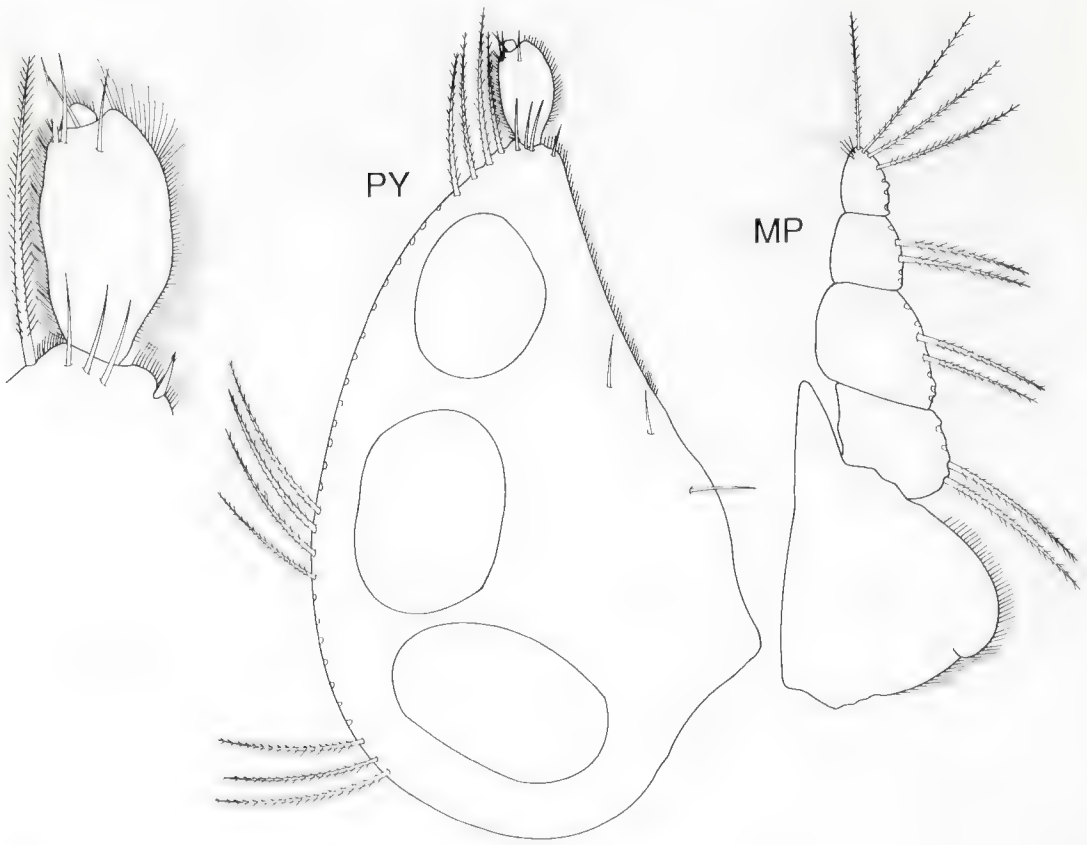


Figure 71. *Gnathia rhytidoponera*. Holotype, QM W19962

McIntyre grab, N. Coleman on FV *Sarda*, Feb 1991 (stn MSL-EG 107), NMV J24631 (2); (stn MSL-EG 106), NMV J24630 (1); (stn MSL-EG 103), NMV J24628 (2); (stn MSL-EG 104), NMV J24629 (1).

*Description*. Total length of holotype: 3.10 mm.

Cephalosome rectangular, 1.1 times as wide as long, lateral margins slightly convex. Eyes well developed, lateral and sessile. Frontal border produced, transverse between mandible; mediofrontal process translucent, with median notch and 3–4 long setae laterally; superior frontolateral process conical, with 5–6 short setae on lateral margin and 4 larger setae near mandible base. External scissura rounded. Supraocular lobe very low, acute. Cephalosome with broad dorsal sulcus; pronounced paraocular tubercles and setae. Antenna 2 longer than antenna 1; flagellum of antenna 1 of 5 articles, without aesthetascs; flagellum of antenna 2 of 7 articles. Mandible elongate, curved; two-thirds length of cephalosome; with unarmed carina; smooth arc-shaped blade on distal two-thirds, produced proximally; seta at midpoint; long, smooth straight basal neck; erisma pronounced. Maxilliped 5-articled; external margins of articles 2–4 bearing plumose setae; palp thin and elongate; endite barely reaching article 3, narrow, with 1 coupling hook. Pylopod 3-articled, elongate and narrow, internal margin of fine short setae; with ring of short, stouter setae posteriorly; article 1 with 9 setae on ventral surface, predominantly along median axis; article 2 elongate, with 12 setae on ventral surface; article 3 minute.

Pereon evenly sided, as wide as cephalosome; margins with numerous setae. Pereonite 1 barely reaching lateral margins dorsally and partially obscured laterally by pereonite 2. Pereonites 2 and 3 subequal, pereonite 4 rectangular, longer than 2 and 3; with anterior constriction. Pereonites 5 and 6 rounded, together as long as others combined. Pereonite 7 not visible. Pleonites 2–4 subequal; posterior border of pleonite 5 produced; pleonal epimera prominent. Pleotelson

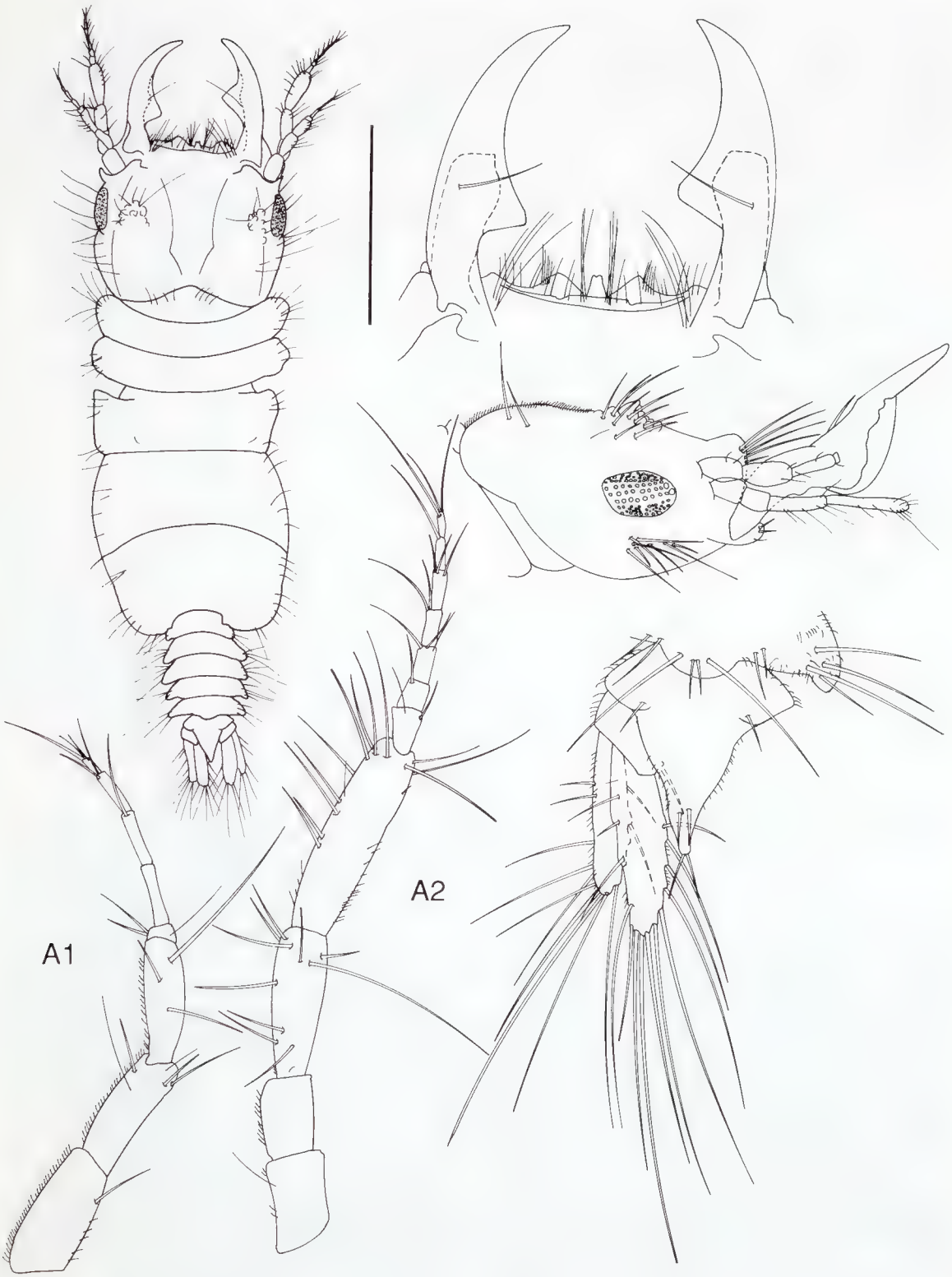


Figure 72. *Gnathia stigmacros*. Holotype, NMV J27576.

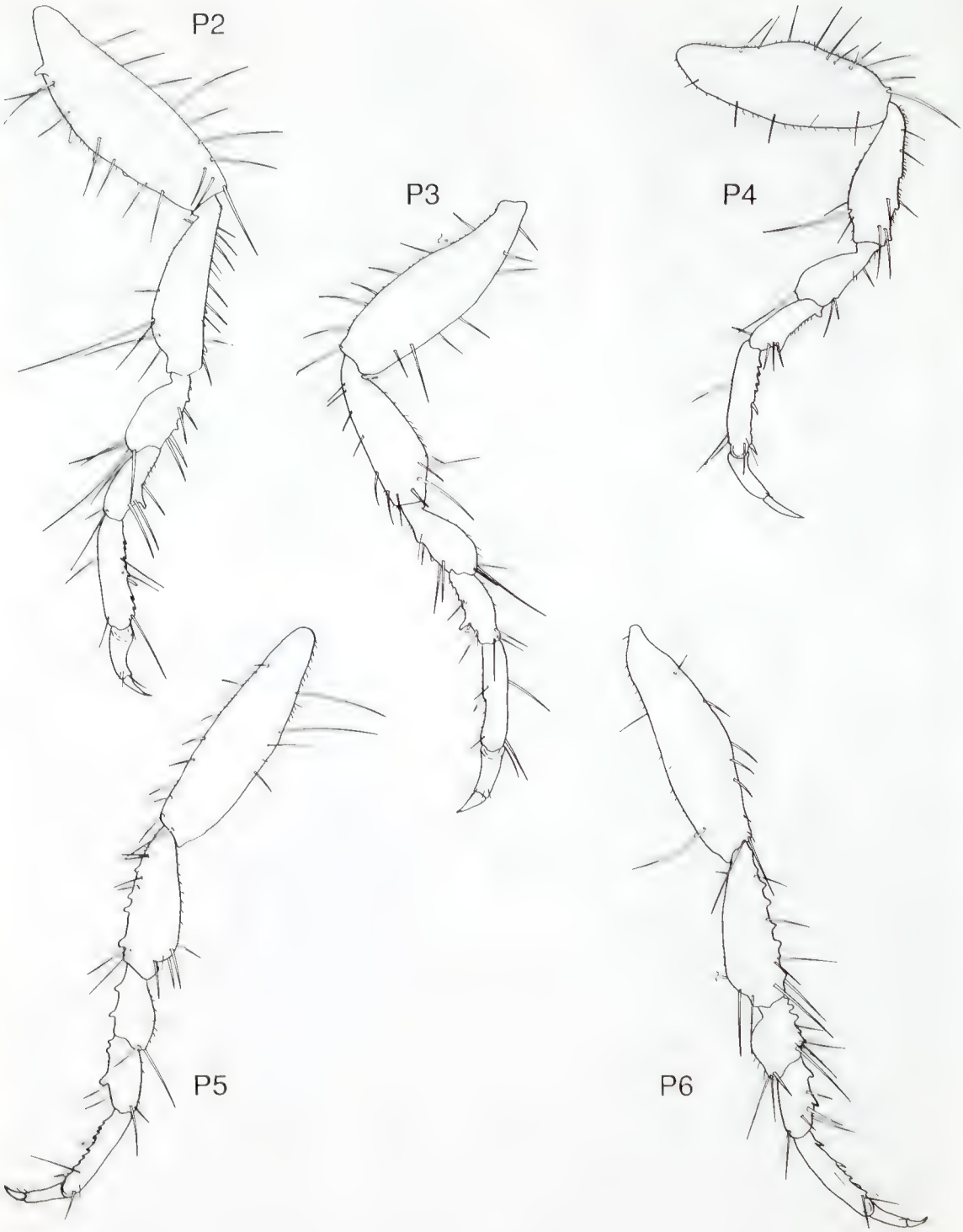


Figure 73. *Gnathia stigmacros*. Holotype, NMV J27576.

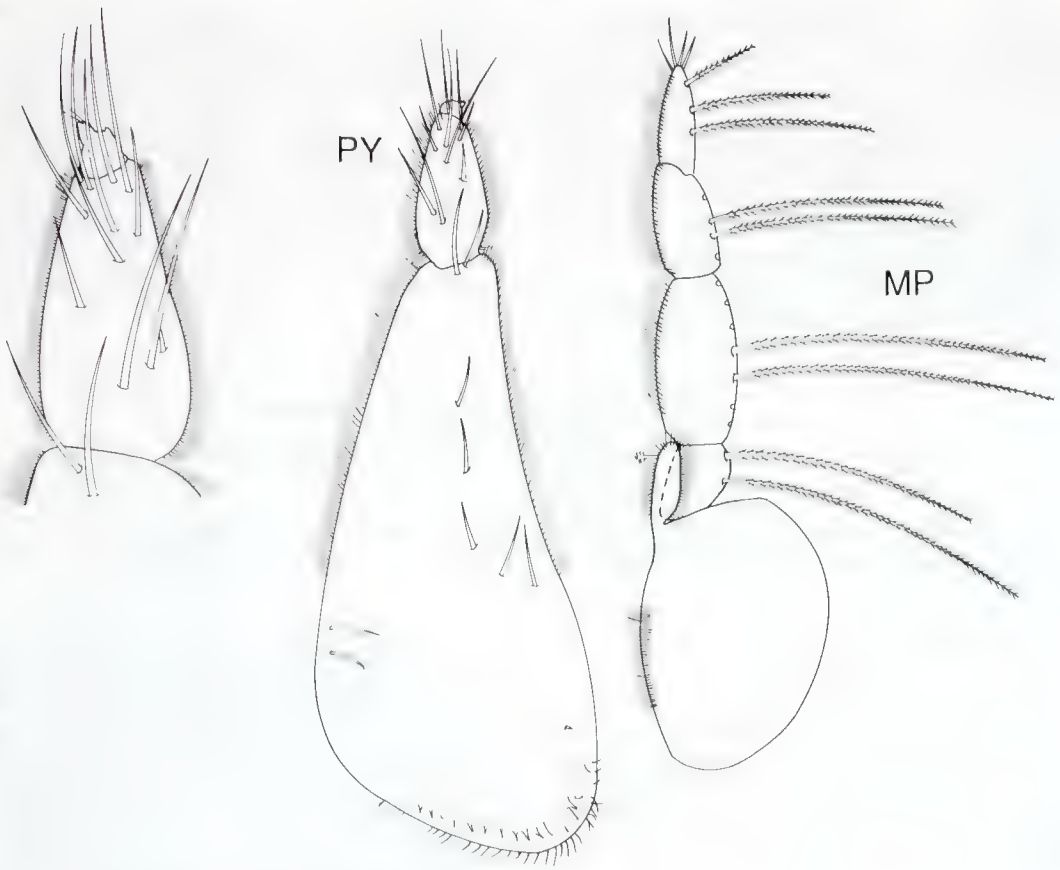


Figure 74. *Gnathia stigmacros*. Holotype, NMV J27576.

subtriangular, longer than wide; lateral margins slightly sinuous; with 2 pairs of simple setae and pair of setae on distal apex. Uropod peduncle without setae; endopod longer than exopod, reaching beyond apex of pleotelson; rami margins with numerous long simple setae.

Pereopods narrow, with few simple setae; ischium to carpus with small lateral projections, particularly on pereopods 5 and 6.

Pleopods setose. Pleopod 2 endopod lacking appendix masculina. Penes 2 small contiguous papillae.

*Distribution.* Victoria, eastern Bass Strait, 27–293 m depth.

*Remarks. Gnathia stigmacros* differs from *G. prolasius* in possessing a completely smooth blade, many setae on the frontal border and more pronounced paraocular tubercles. *G. stigmacros* resembles *G. malaysiensis* Müller in the shape of the mediofrontal process and the mandible but is easily distinguished by its much shorter superior frontolateral processes and relatively straight frontal border.

***Monodgnathia*** gen. nov.

*Type species. Monodgnathia ponera* sp. nov.

*Diagnosis.* Eyes absent. Frontal border produced as distinct delineated region (chalky white in Australian species); without processes. Mandible with occluding, smooth mandibular blade. Pereonite 1 immersed in cephalon. Pylopod 5-articled; operculate, article 2 enlarged; article 3 with spines; lacking plumose setae on external margin. Pereopod 4 basis with anterior quadrate lobe and ischium distally expanded into circular cusp.

*Etymology.* For Théodore Monod whose monumental 1926 work on Gnathiidae has become a classic study of a family of Isopoda.

*Remarks. Monodgnathia* and *Bathygnathia* are closely related genera (see cladogram) with

almost identical pylopods. Both genera possess a 5-articled, operculate pylopod with greatly enlarged second article and a minute fifth article. *Monodgnathia* is characterised by the presence of a curved mandible with a smooth mandibular blade, a distinct frontal border which is not produced into a rostrum and the absence of a protruding buccal cavity wall. Four species are recognised, two newly described and two transferred from *Akidognathia*. Remaining species of *Akidognathia* are now members of *Bathygnathia* of which *Akidognathia* is now a junior synonym. *Akidognathia poteriophora* Monod, 1926 is tenatively placed in the new genus on the basis of the mandible and rostrum although the pylopod is not operculate and the basis of pereopod 4 lacks the anterior quadrate lobe. The pylopod, maxilliped and fusion of pereonites 5 and 6 suggest that *A. poteriophora* is a subadult specimen with some features not fully developed but it must be stressed that this conclusion has been reached based on the literature.

**Key to males of *Monodgnathia* from Australia**

1. Frontal border produced medianly, lacking setae; cephalon lacking projections covering base of mandibles ..... *M. ponera*

— Entire frontal border produced, with setae; cephalon with quadrate projections covering base of mandibles ..... *M. colobostruma*

***Monodgnathia colobostruma*** sp. nov.

Figures 75–77

*Material examined.* Holotype. Victoria, S of Point Hicks (38°21.9'S, 149°20.0'E), 1000 m, WHOI epibenthic sled, G.C.B. Poore et al. on ORV *Franklin*, 23 Jul 1986 (stn SLOPE 32), NMV J19115 (1 male).

*Description.* Total length of holotype: 6.97 mm.

Cephalosome rectangular, 1.25 times as long as wide, lateral margins convex. Eyes absent. Entire frontal border produced, truncated, with 6 large setae medianly and 4–5 smaller setae spreading submarginally; distinct chalky white region between mandibles at end of short dorsal sulcus. Cephalosome with low posterior median tubercle and distinct quadrate cover over base of mandible. Antenna 2 longer than antenna 1; flagellum of antenna 1 of 5 articles, with 3 aesthetases; flagellum of antenna 2 of 7 articles. Mandible half length of cephalosome; apex curved inwards; with unarmed carina; smooth occluding blade proximally and flat dorsal lobe, proximally. Maxilliped 5-articled; external margins of articles 2–4 bearing plumose setae; endite clearly reaching article 3, with 6 coupling hooks. Pylopod 5-articled, with many simple setae medianly, mainly on articles 3 and 4; articles 2 and 3 with large areolae; article 3 with 2 pectinate spiniform setae on external anterolateral margin; article 5 minute.

Pereon evenly sided, slightly wider than cephalosome; pereonites progressively longer. Pereonite 1 dorsally small, not reaching lateral margins of pereon and partially obscured laterally by pereonite 2. Pereonite 4 with slight anterior constriction and median groove. Pereonite 5 with dorsal sulcus and areae laterales. Pereonite 6 with lobi laterales and small lobuii. Pereonite 7 small, a thin band; overlapping pleon. Pleonites similar, pleonite 5 slightly longer than others; pleonal epimera prominent. Pleotelson subtriangular, as wide as long; lateral margins slightly sinuous with 5–6 pairs of simple setae laterally and 1 medianly. Uropodal peduncle with 2 setae; rami of subequal length, reaching apex of pleotelson; internal margins of rami bearing few plumose setae.

Pereopods 2 and 3 less robust than others, with dense cover of simple setae; others with moderate cover of simple setae; pereopod 4 basis with pronounced anterior quadrate lobe, ischium distally expanded as flat, circular projection with 4 large tubercles; carpus to unguis extending at right angle to basal pereopod, forming a surface with circular cusp of ischium.

Pleopods with short marginal setae. Pleopod 2 endopod with appendix masculina subequal to length of rami. Penes 2 contiguous papillae.

*Distribution.* Eastern Bass Strait slope, 1000 m depth.

*Remarks. Monodgnathia colobostruma* and *M. ponera* are the first records of this genus from Australian waters. *M. colobstruma* and the other members of this genus differ from the only known specimen of *M. poteriophora* (which we believe to be a subadult specimen – see *Monodg-*

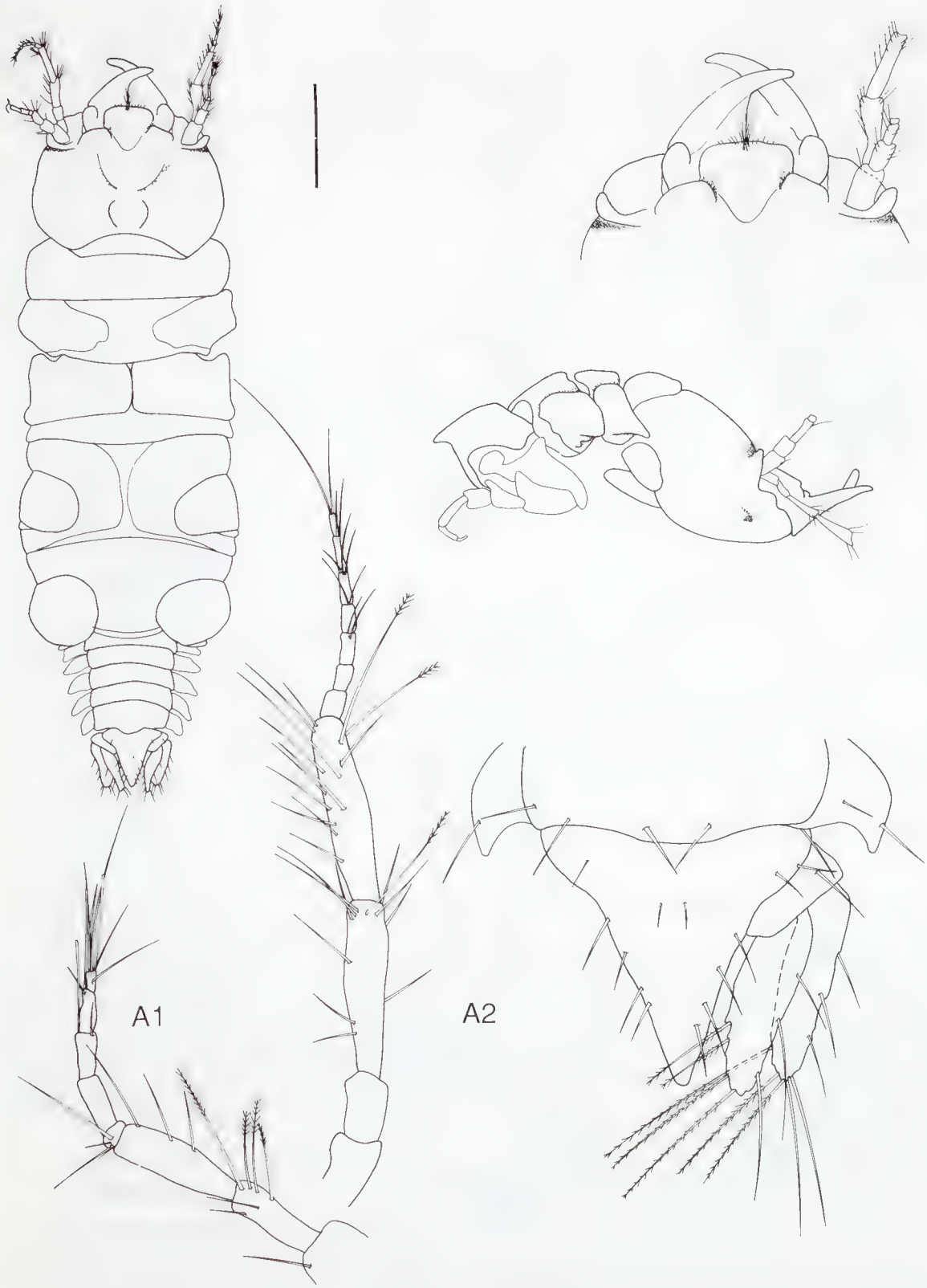


Figure 75. *Monodgnathia colobostruma*. Holotype, NMV J19115.


Figure 76. *Monodgnathia colobostruma*. Holotype, NMV J19115.

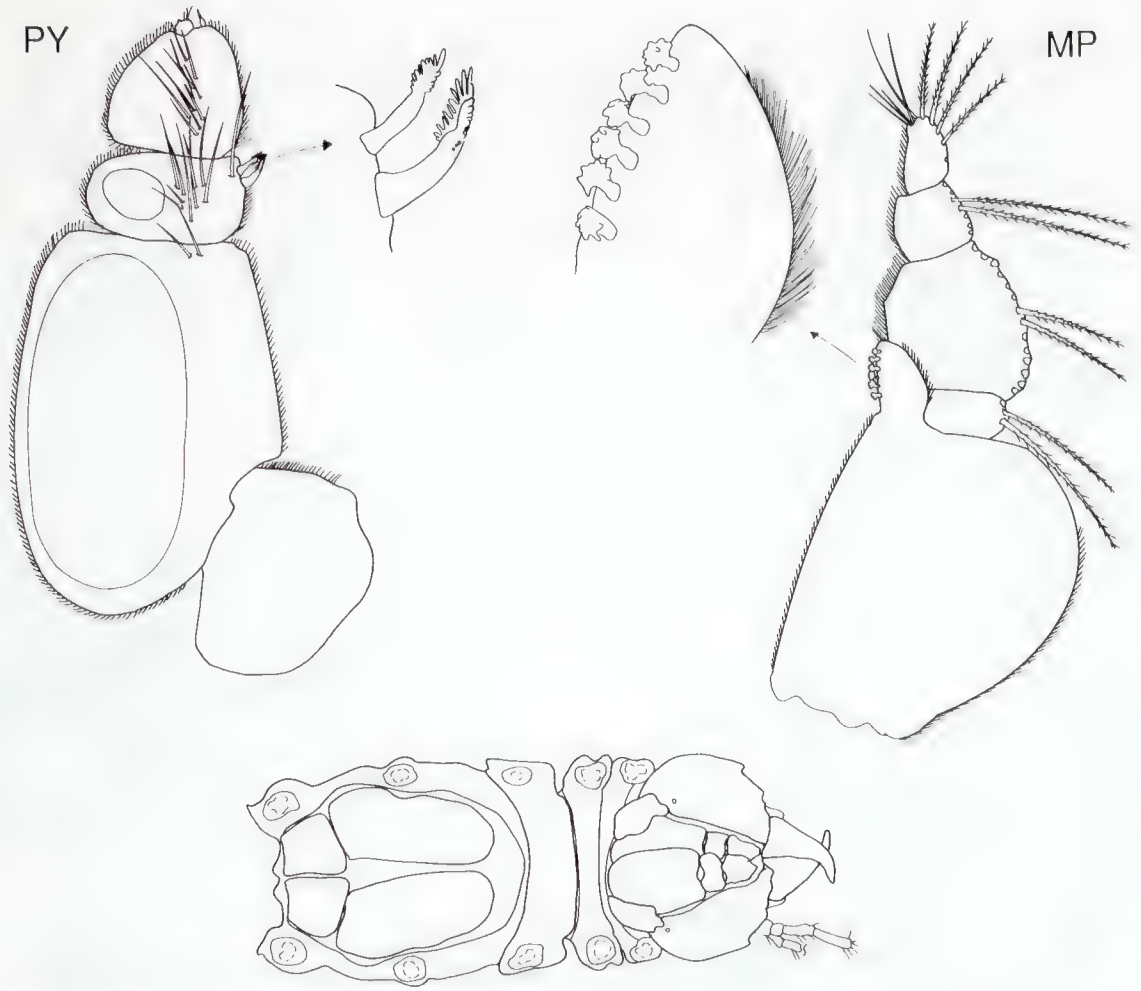


Figure 77. *Monodgnathia colobostruma*. Holotype, NMV J19115.

*nathia* remarks) in possessing a operculate pylopod and lacking fused pereonites 5 and 6.

*M. colobostruma* possesses a more robust habitus than other species of *Monodgnathia* and is characterised by a square frontal border produced across its entire length, not only between the base of the mandibles; raised protrusions on the cephalon at the base of the mandibles and slight dorsal lobes on the mandibles.

### ***Monodgnathia ponera*** sp. nov.

Figures 78–80

*Material examined.* Holotype. Lord Howe Rise, southwestern Pacific Ocean (29°13.3′S, 160°35.4′E), 1550 m, epibenthic sled, Australian Musuem party on ORV *Franklin*, 4 May 1989 (stn 05/89 site 20), AM P41294 (1 male).

*Description.* Total length of holotype: 11.98 mm.

Cephalosome rectangular, 1.4 times as wide as long, lateral margins convex. Eyes absent. Frontal border produced, smoothly rounded as a distinct chalky white region, devoid of setae. External scissura rounded. Supraocular lobe smoothly convex. Cephalon with 2 small depressions medianly; anterior one larger at base of short sulcus; smaller posterior one near anterior border of peronite 1. Antenna 2 longer than antenna 1; flagellum of antenna 1 of 5 articles, with 3 aesthetascs; flagellum of antenna 2 of 8 articles. Mandible subequal to length of cephalosome; apex curved inwards; with unarmed carina; slight mandibular incisor one-third way along; small basal neck obscured dorsally by rostrum; blades smooth proximally,

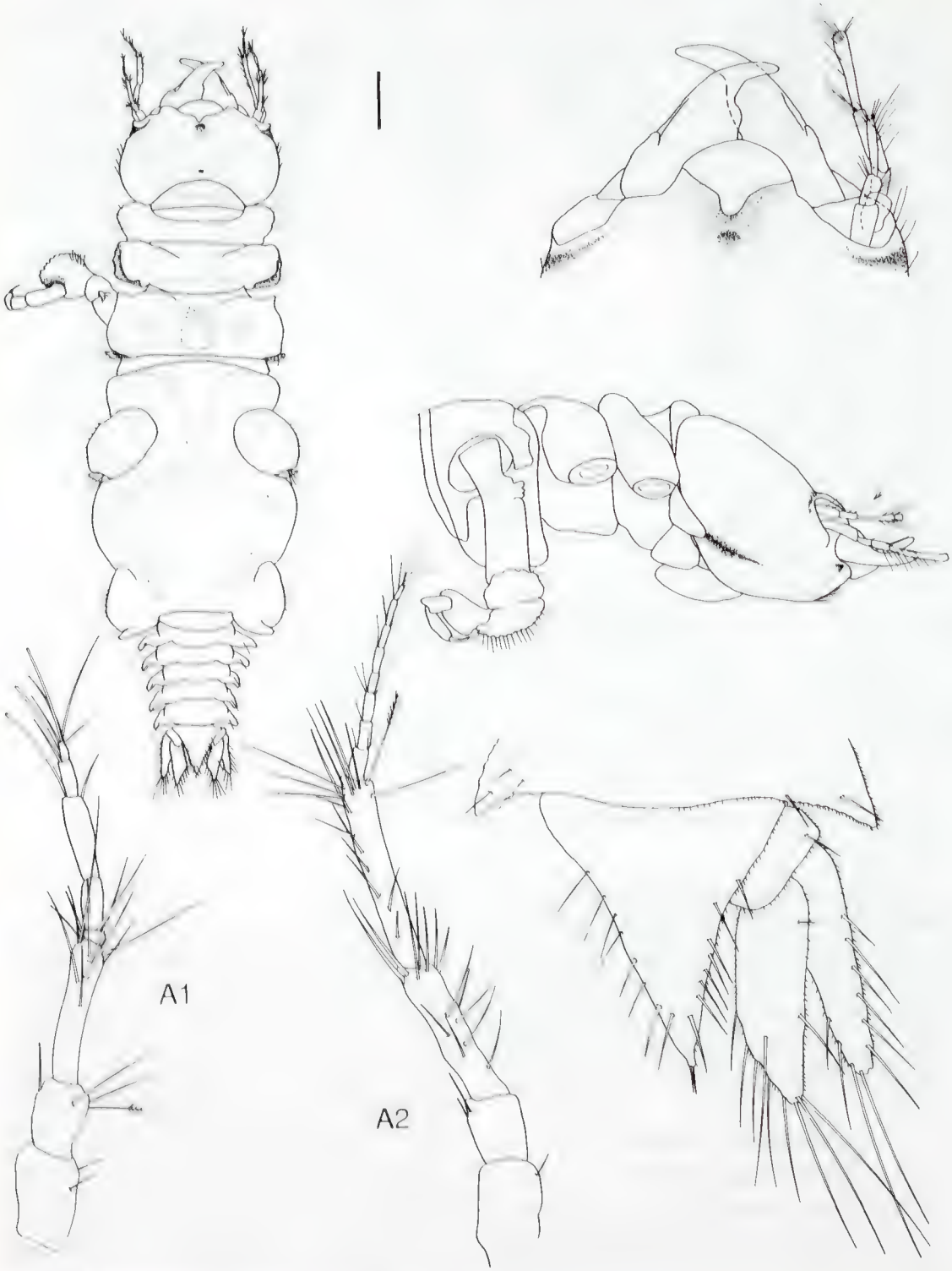


Figure 78. *Monodgnathia ponera*. Holotype, AM P41294.

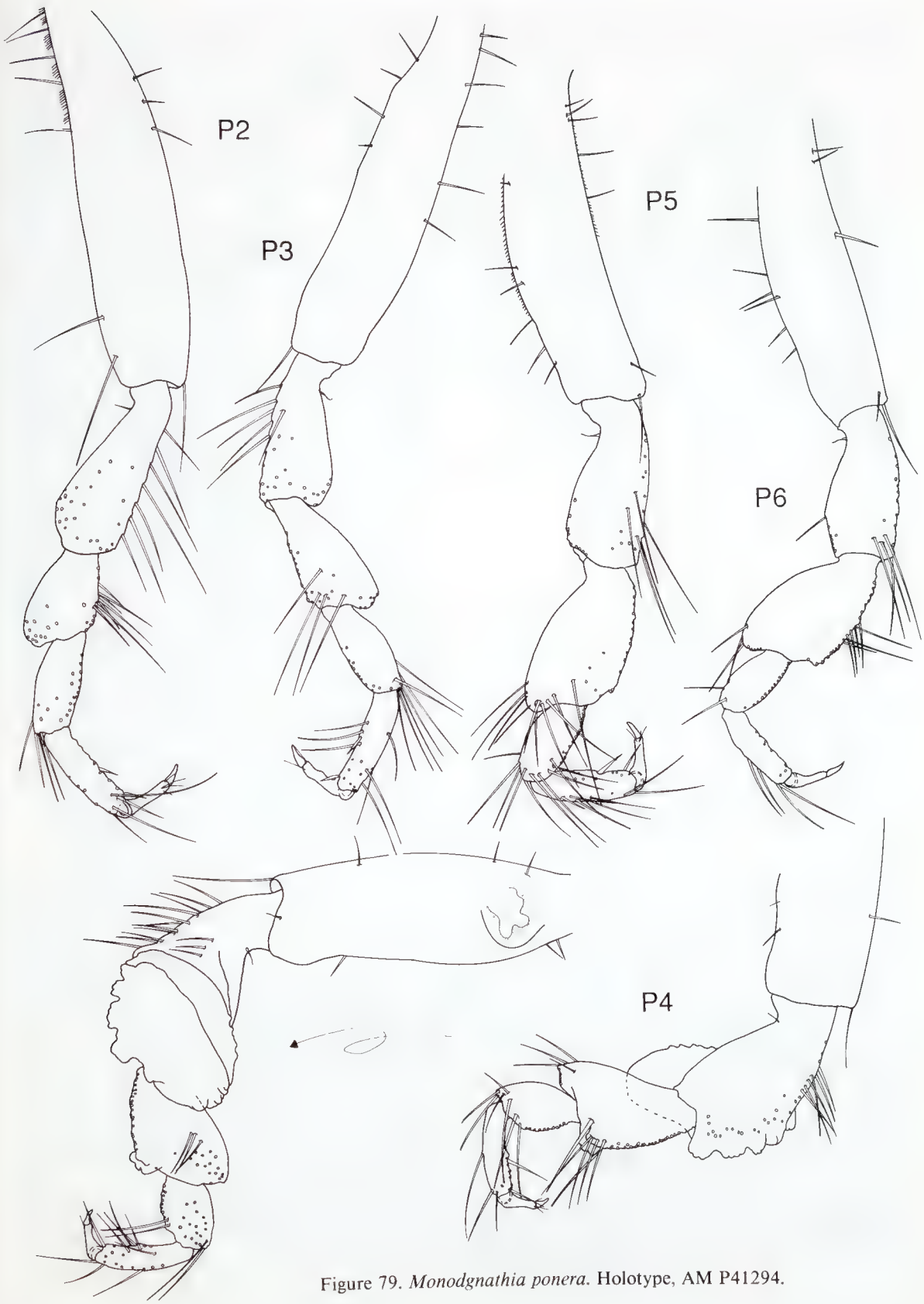


Figure 79. *Monodgnathia ponera*. Holotype, AM P41294.


Figure 80. *Monodgnathia ponera*. Holotype, AM P41294.

occluding. Maxilliped 5-articled; external margins of articles 2–4 bearing plumose setae, article 2 short; endite clearly reaching article 3, narrow, with 6 coupling hooks. Pylopod 5-articled, with many simple setae medianly, from distally on article 2 to base of article 5; article 3 with at least 1 pectinate spiniform seta on internal anterolateral margin (second seta damaged distally); article 5 minute.

Pereon widest posteriorly at peronites 5 and 6, 1.25 times as wide as cephalosome; pereonites length and width increasing progressively. Pereonite 1 produced slightly, barely reaching lateral margins dorsally and partially obscured laterally by pereonite 2. Pereonite 4 with anterior constriction, median groove as bilobed sulcus. Pereonite 5 with dorsal sulcus and areae laterales. Pereonite 6 with small lobi laterales and pronounced lobuii; pereonites 5 and 6 longer than other pereonites combined. Pereonite 7 very narrow, overlapping pleon. Pleon progressively narrower, epimera prominent. Pleotelson subtriangular, longer than wide; lateral margins slightly sinuous; with 8 pairs of simple setae laterally and pair of small setae on distal apex. Uropodal peduncle with 1 seta; rami subequal, reaching beyond apex of pleotelson, bearing long simple setae.

Pereopods with dense cover of simple setae particularly on ischium to dactylus; pereopod 4 basis with anterior quadrate lobe, ischium distally expanded as flat, large circular cusp-shaped projection with 4–5 large tubercles; carpus to unguis extending at right angle to basis, forming surface with circular cusp of ischium.

Pleopods without setae. Pleopod 2 endopod with appendix masculina three-quarters length of rami. Penes 2 contiguous papillae.

*Distribution.* South-western Pacific Ocean, 1550 m depth.

*Remarks. M. ponera* most resembles *M. cristatipes* (Stebbing). Both species possess a smoothly rounded frontal border that protrudes between the mandibles; relatively simple mandibles; and pronounced lobuii. *M. ponera* differs from *M. cristatipes* principally in the proportions of the cephalon. *M. cristatipes* possesses a rounded cephalon while the cephalon of *M. ponera* is more rectangular.

### ***Paragnathia*** Omer-Cooper and Omer-Cooper

*Paragnathia* Omer-Cooper and Omer-Cooper, 1916: 26. — Omer-Cooper 1916: 124. — Monod, 1926: 308.

*Metagnathia* Monod, 1922: 645 (type species: *Anceus formica* Hesse, 1864).

*Type species. Anceus halidaii* Bate and Westwood, 1868 (original designation), junior subjective synonym of *Anceus formica* Hesse, 1864.

*Diagnosis.* Eyes present. Frontal margin of cephalon produced, without processes. Mandibles with simple crenulate blade. Pereonite 1 immersed in cephalon. Pereonite 4 with anterior constriction. Pylopod 6-articled; operculate (articles 1, 3 and 4 enlarged, article 2 reduced); without margin of plumose setae. Pleonites without setae.

*Remarks. Paragnathia* is a monotypic Afro-European genus, the only species being *P. formica* (Hesse, 1864). The species has a complex synonymy (Monod, 1926). It is the only species of Gnathiidae with an operculate, 6-articled pylopod with a reduced second article and mandibles with a crenulate blade.

### ***Thaumastognathia*** Monod

*Thaumastognathia* Monod, 1926: 304.

*Type species. Thaumastognathia diceros* Monod, 1926 (monotypy).

*Diagnosis.* Eyes present. Frontal border variable. Mandibles strongly curved with a crenulate blade. Antenna 1 with stout peduncle, antenna 1 longer than antenna 2. Pereonite 1 immersed in cephalon. Mouthparts small, no articles enlarged. Pylopod 4- or 5-articled, pediform, not operculate. Maxilliped highly reduced or absent. Pereon smooth, cephalosome quasipentagonal, pereonite 7 not visible dorsally. Pleon often folded under peron.

*Remarks. Thaumastognathia* is characterised by the very small size of the pylopod which can be clearly seen only under a compound micoscope, and the reduction or absence of the maxilliped; pereon smooth, cephalosome quasipentagonal, antennae curved under the mandibles, antennae 1 longer than antenna 2, absence of pereonite 7, and the pleon folded under the pereon.

These are the first records of *Thaumastognathia* since Monod (1926) described the type species, *T. diceros*, from New Zealand. The three new species bring the total number of species to four, all found in Australasia. A specimen belonging to another species of *Thaumastognathia* was collected from north Queensland but was not described because of its poor condition. All species of *Thaumastognathia* are small, less than 2.5 mm long.

**Key to males of species of *Thaumastognathia***

1. Mandibles with pronounced mandibular incisura; pleotelson tapering, margins deeply concave ..... *T. wasmannia*

— Mandibles without mandibular incisura; pleotelson subtriangular, margins straight or slightly sinuous ..... 2

2. Frontal border slightly excavated, maxillipeds absent ..... *T. metaphone*

— Frontal border produced, maxillipeds present ..... 3

3. Ventral margin of cephalon with pair of strong projections lateral to mandibles; carpi of pereopods with row of even spines ..... *T. diceros*

— Ventral margin of cephalon without strong projections; carpi of pereopods with uneven spination ..... *T. orectognathus*

***Thaumastognathia metaphone*** sp. nov.

Figures 81, 82

*Material examined.* Holotype. South Australia. Pearson I., E side in bay (33°57.30′S, 134°15.70′E), 20 m, bryozoans, sponges etc. on shaded surface, SCUBA, G.C.B. Poore, 17 Apr 1985 (stn SA 55), NMV J27570 (1 male).

Paratype. Type locality, NMV J27560 (1 male).

*Description.* Total length of holotype: 2.51 mm.

Cephalosome quasipentagonal, 2.3 times as wide as long, lateral margins slightly concave. Eyes well developed, lateral and sessile. Frontal border roughly transverse, excavated medianly; mediofrontal process small, rounded, located at base of excavation; superior frontolateral process smoothly rounded, forming lateral border for median excavation, with 5–6 setae submarginally spreading laterally, along slight excavation at base of mandible. Inferior frontolateral process conical, mostly transparent, directly ventral to superior frontolateral process. Supraocular lobe not pronounced. Antennae stout, curved under mandible, antenna 1 longer than 2; flagellum of antenna 1 of 3 articles, with 2 aesthetases; flagellum of antenna 2 of 3 articles, shorter than last article of peduncle. Mandible strongly curved, depressed in lateral view, half length of cephalosome; with unarmed carina; slight incisura; dentate blade slightly produced on proximal half; seta at midpoint. Maxilliped absent. Pylopod thin, elongate, 5-articled, first and third with seta, fifth minute.

Pereon oval, wider than cephalosome. Pereonite 1 dorsally small, not reaching lateral margins and partially obscured laterally by pereonite 2. Peronites 2, 3 and 4 progressively longer. Pereonites 5 and 6 fused, longer than others together. Pereonite 7 not visible dorsally. Pleon folded under pereon, pleonite 5 almost as wide but longer than other pleonites, all without setae. Pleotelson subtriangular, wider than long with pair of simple setae laterally and pair of setae on distal apex. Uropodal peduncle without setae, endopod twice as long as exopod, not reaching apex of pleotelson, with 4 setae distally and 1 seta laterally; exopod with 3 distal setae.

Pereopods with posterior and lateral faces of ischium-carpus with irregular acute projections, elsewhere few simple setae.

Pleopods without setae. Pleopod 2 endopod lacking appendix masculina. Penes 2 small contiguous papillae.

*Distribution.* South Australia, rocky substrate, 20 m depth.

*Remarks. Thaumastognathia* is characterised by an oval pereon, cephalosome with concave posterolateral margins and a pleon curving under the pereon. *T. diceros* Monod from New Zealand is easily distinguishable from *T. metaphone* and the other newly described species by the frontal, horn-like protrusions. *T. metaphone* is characterised by the slight median indentation of the frontal border.

***Thaumastognathia orectognathus*** sp. nov.

Figures 83, 84

*Material examined.* Holotype. Victoria, central Bass Strait, 66 km S of Rodondo I., (39°48.6′S, 146°18.8′E), 82 m, sand-silt-mud, WHOI epibenthic sled, R.S. Wilson on RV *Tangaroa*, 13 Nov 1981 (stn BSS 158), NMV J27567 (1 male).

Paratypes. Most collected using WHOI epibenthic sled by R.S. Wilson on RV *Tangaroa*, Nov 1981, Tasmania. Central Bass Strait, 9 km SSW of Cape Adansan, Three Hummock I. (40°30.9′S, 144°56′E), 27 m,

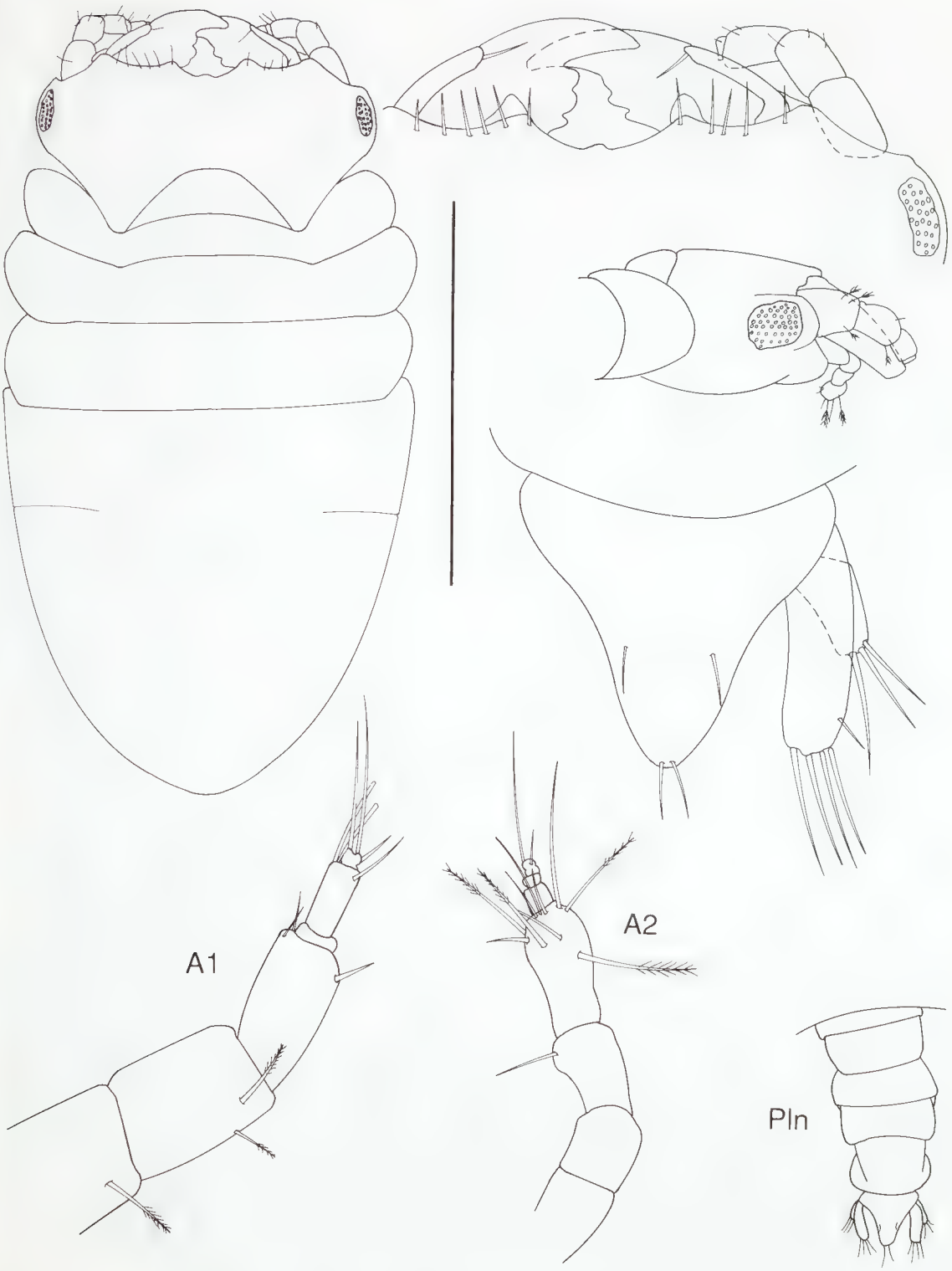


Figure 81. *Thaumastognathia metaphone*. Holotype, NMV J27570.

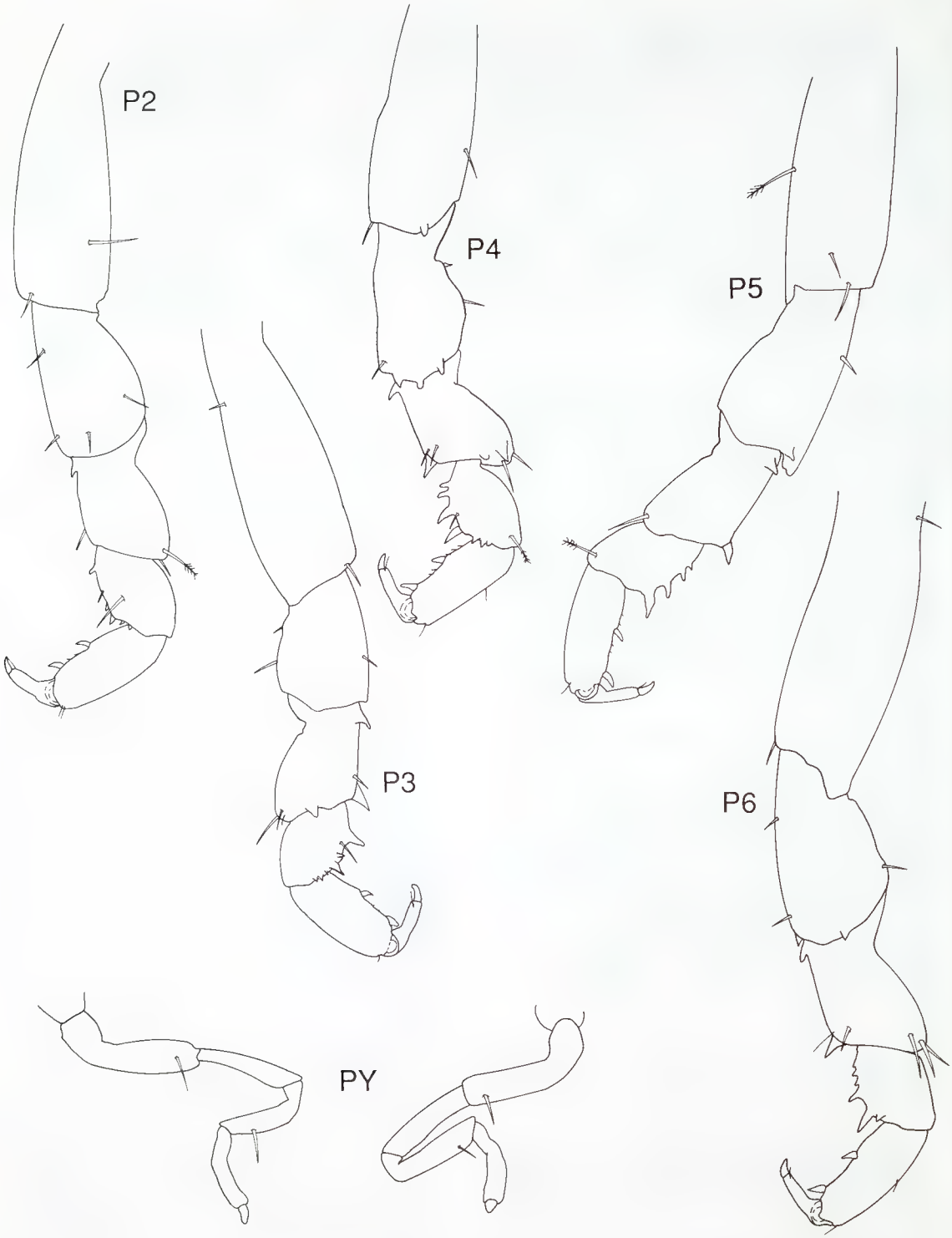


Figure 82. *Thaumastognathia metaphone*. Holotype, NMV J27570.

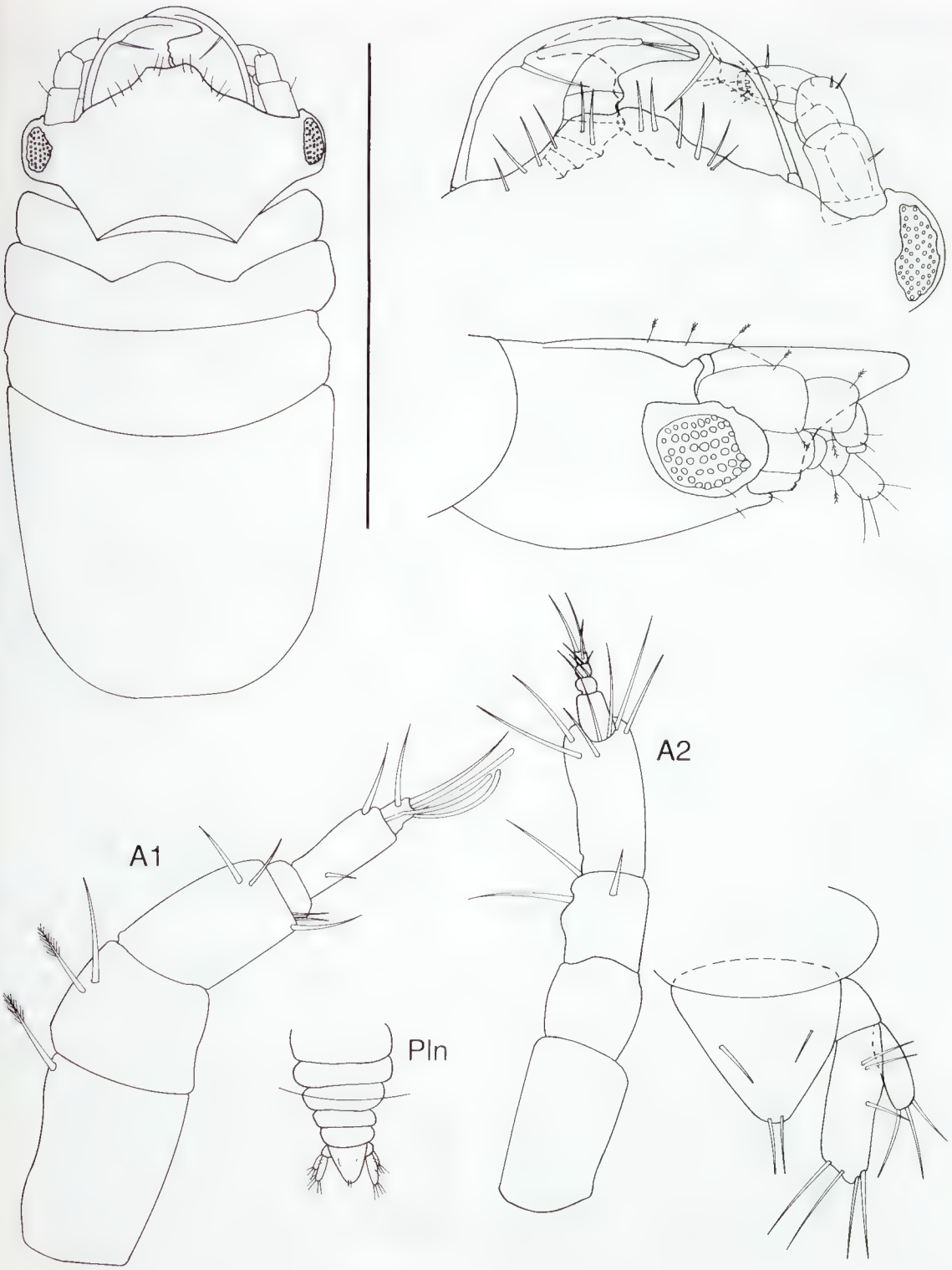


Figure 83. *Thaumastognathia orectognathus*. Holotype, NMV J27567.

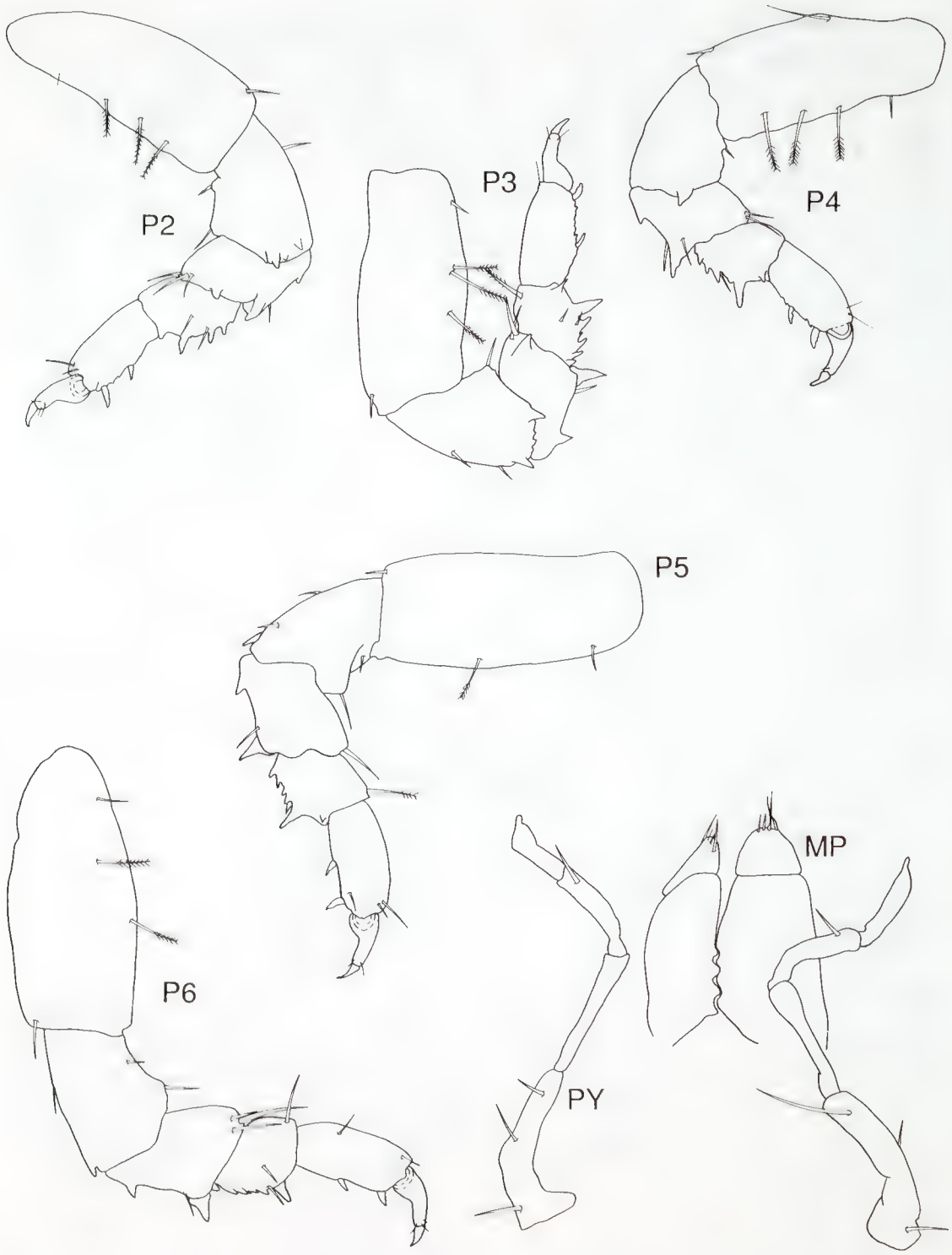


Figure 84. *Thaumastognathia orectognathus*. Holotype, NMV J27567.

very coarse sand, 2 Nov 1980 (stn BSS 109), NMV J8356 (1). Eastern Bass Strait, 100 km NE of North Point, Flinders I., (38°52.6′S, 148°25.2′E), 130 m, fine sand, (stn BSS 170), NMV J8361 (1). 85 km NE of North Point, Flinders I. (39°02.4′S, 148°30.6′E), 120 m, muddy sand (stn BSS 169), NMV J8355 (1).

Victoria. Central Bass Strait, 66 km S of Rodondo I. (39°48.6′S, 146°18.8′E), 82 m, sand-silt-mud (stn BSS 158), NMV J8360 (3). Eastern Bass Strait, 43 km SE of Port Albert (38°53.7′S, 147°06.5′E), 58 m, coarse shell (stn BSS 177), NMV J8358 (1), NMV J8357 (2). 14.3 km WSW of Pt Ricardo (37°50.74′S, 148°28.40′E), 32 m, rock-sand-mud, Smith-McIntyre grab, Marine Science Laboratories on RV *Sarda*, 26 Sep 1990 (stn MSL-EG 46), NMV J24632 (4).

Other material. Bass Strait, 15 km S of Cape Wellington, (39°03.2′S, 146°39.5′E), 55 m, muddy fine sand (stn BSS 179), NMV J8359 (2); S of Point Hicks (38°14.80′S, 149°9.30′E), 200 m, coarse sand (stn SLOPE 41), NMV J19124 (2).

*Description.* Total length of holotype: 1.50 mm.

Cephalosome quasipentagonal, 1.8 times as wide as long, lateral margins slightly concave. Eyes well developed, lateral and sessile. Frontal border produced dorsally with slightly excavate truncate midanterior margin, with 6 setae submarginally each side. Supraocular lobe not pronounced. Antennae stout, subequal, curved under mandible; flagellum of antenna 1 of 3 articles, with 4 aesthetascs; flagellum of antenna 2 of 4 articles, shorter than last article of peduncle. Mandible strongly curved, half length of cephalosome; with unarmed carina; without incisura; crenulate blade produced on proximal half; seta at midpoint. Maxilliped very reduced, of 2 articles; first with crenulate mesial margin, second much shorter, with 4 apical setae. Pylopod thin, elongate, of 4 articles, first with 3 setae, third with 1 seta.

Pereon oval-rectangular, as wide as cephalosome. Pereonite 1 dorsally small, not reaching lateral margins and not visible laterally. Pereonites 2, 3 and 4 progressively longer. Pereonites 5 and 6 fused, longer than others together. Pereonite 7 not visible dorsally. Pleon folded under pereon, pleonites similar, progressively narrower, all without setae. Pleotelson subtriangular, wider than long, with pair of simple setae laterally and pair of setae on apex. Uropodal peduncle without setae, endopod twice as long as exopod, reaching beyond apex of pleotelson, dorsolaterally with 3 setae, distally with 4 setae, exopod with 3 distal setae.

Pereopods 2–6 bases with plumose setae on anterior margins, elsewhere few simple setae, posterior and lateral faces of ischium-carpus with irregular acute projections, propodus palms with 2 short spiniform setae.

Pleopods without setae. Pleopod 2 endopod lacking appendix masculina. Penes 2 small contiguous papillae.

*Distribution.* Central and eastern Bass Strait, 27–200 m depth.

*Remarks. Thaumastognathia orectognathus* is most easily recognised by its produced frontal border.

***Thaumastognathia wasmannia*** sp. nov.

Figures 85, 86

*Material examined.* Holotype. Tasman Sea, 20 km E of Falmouth, Tasmania (41°32.9′S, 148°35.0′E), 122 m, WHOI epibenthic sled, R.S. Wilson on RV *Soela*, 10 Oct 1984 (stn S05/84 5), NMV J27579 (1 male).

Paratype. Type locality, NMV J27559 (1 male).

*Description.* Total length of holotype: 1.73 mm.

Preserved specimen opaque. Cephalosome quasipentagonal, 2.5 times as wide as long, lateral margins slightly concave. Eyes well developed, lateral and sessile. Frontal border transverse, produced very slightly at base of mandible with shallow excavate midanterior margin, 5 setae submarginally each side forming slight arc. External scissura very shallow. Supraocular lobe not pronounced. Antennae stout, subequal, curved under mandible; flagellum of antenna 1 of 2 articles, with 2 aesthetascs; flagellum of antenna 2 of 4 articles, shorter than last article of peduncle. Mandible strongly curved, two-thirds length of cephalosome; with unarmed carina; pronounced mandibular incisor about 0.2 length of mandible, thin and very translucent; crenulate blade weakly produced on proximal two-thirds; setae one-third way along. Maxilliped absent. Pylopod thin, elongate, of 4 articles, first with 2 or 3 setae.

Pereon oval, wider than cephalosome. Pereonite 1 dorsally small, not reaching lateral margins and partially obscured laterally by pereonite 2. Pereonite 4 longer than 2 and 3. Peronites 5 and 6 weakly fused, longer than others together. Pereonite 7 not visible dorsally. Pleon folded under pereon, pleonites 4 and 5 as wide and longer than anterior ones, all without setae. Pleotelson elongate, sharply tapering, as wide as long, lateral margins deeply concave with 2 pairs of simple setae medianly and pair of setae on distal apex. Uropodal peduncle with 1 seta, rami subequal, reaching just beyond apex of pleotelson; endopod dorsolaterally with 3 setae, distally

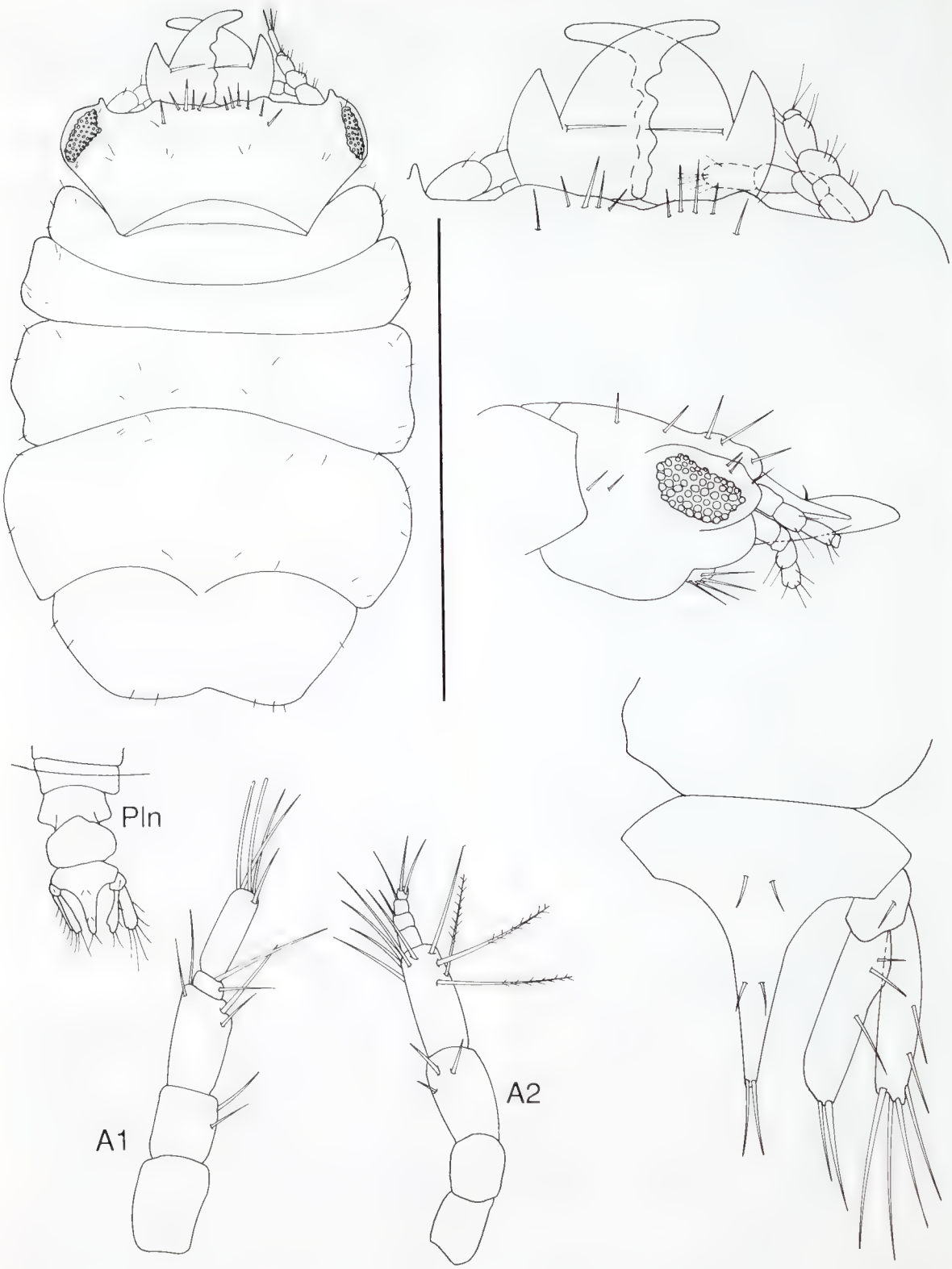


Figure 85. *Thaumastognathia wasmannia*. Holotype, NMV J27579.

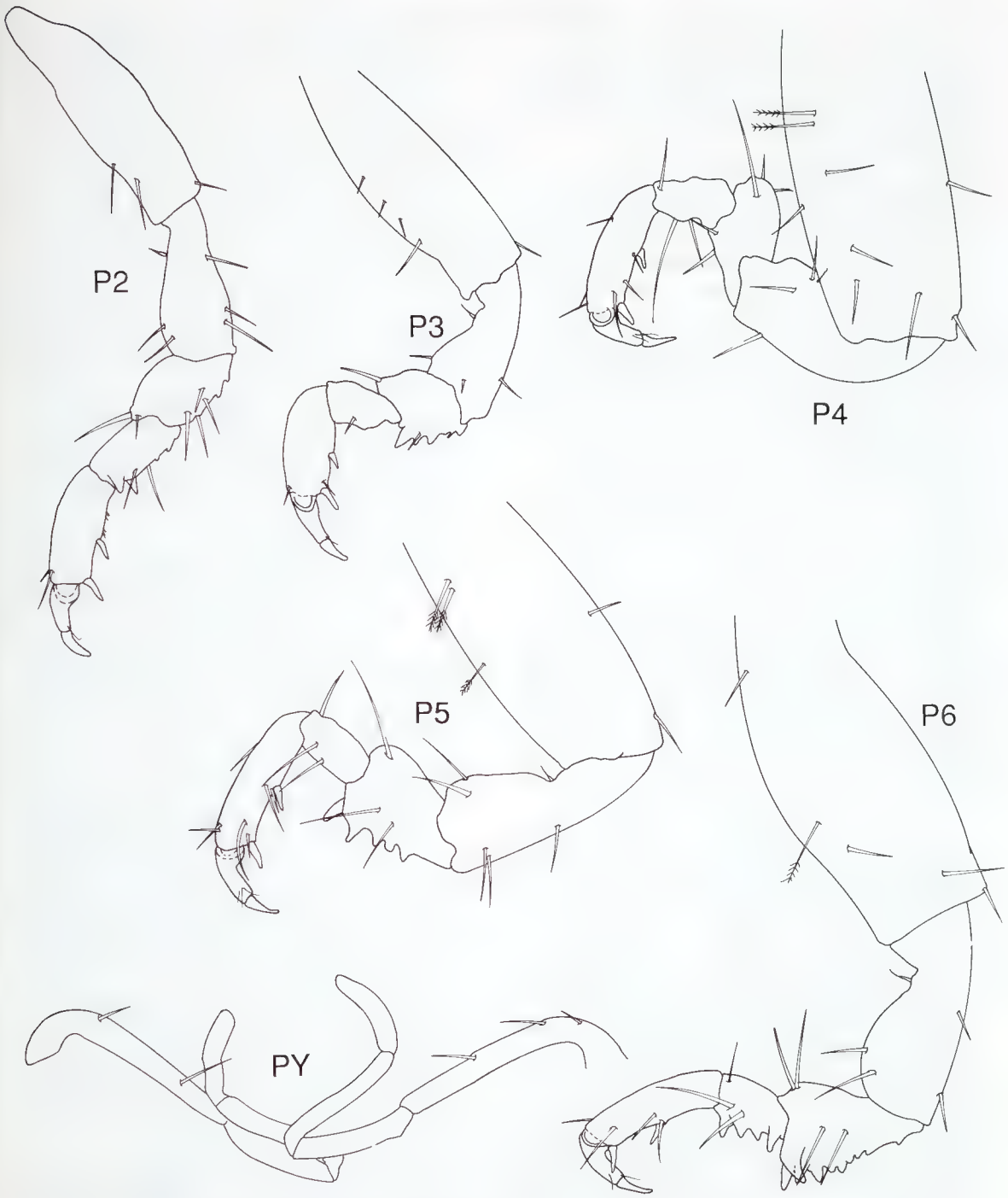


Figure 86. *Thaumastognathia wasmannia*. Holotype, NMV J27579.

with 2 setae; exopod with 3 lateral and 3 distal setae.

Pereopods 4–6 larger than 2 and 3; their bases with few plumose setae on anterior margins, elsewhere few simple setae; posterior and lateral faces of merus-carpus with irregular acute projections, most pronounced on pereopod 6.

Pleopods without setae. Pleopod 2 endopod lacking appendix masculina. Penes 2 small contiguous papillae.

*Distribution.* Eastern Tasmania, 122 m depth.

*Remarks. T. wasmannia* is characterised by pronounced mandibular incisors, relatively straight frontal border and deeply concave lateral margins on the pleotelson.

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# FOUR NEW GENERA OF MARINE ISOPOD CRUSTACEANS (SPHAEROMATIDAE) FROM EASTERN AND SOUTHERN AUSTRALIA

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**Abstract**

Bruce, N.L., 1994. Four new genera of marine isopod crustaceans (Sphaeromatidae) from eastern and southern Australia. *Memoirs of the Museum of Victoria* 54(2): 399–438.

Four new genera of sphaeromatid isopods (subfamily Sphaeromatinae) are described: *Benthosphaera* gen. nov., *Xynosphaera* gen. nov., *Bregmotypta* gen. nov., and *Cercosphaera* gen. nov. *Benthosphaera* is recorded from tropical north-eastern Australia (off Townsville), to south-eastern Australia (off Tasmania), and is represented by *Benthosphaera arkoola* sp. nov. (type species), *B. guaware* sp. nov. and *B. reburra* sp. nov. The genus occurs at depths between 150 and 1200 metres. *Xynosphaera colemani* gen. et sp. nov. is recorded burrowing into Alcyonacea stems, from the northern Great Barrier Reef, the Philippines and Madagascar. *Bregmotypta* gen. nov. is characterized by the anterior margin of the head being greatly elongated. The genus is recorded from the central New South Wales coast (*B. pavicula* sp. nov.) and an undescribed species also occurs in the southern Great Barrier Reef.

*Cercosphaera* gen. nov. is represented by five species, three described here: *Cercosphaera wirritin* sp. nov. (type species), *C. dilkera* sp. nov. and *C. coloura* sp. nov. The genus is recorded from shallow water habitats to a depth of 50 m, and its range extends from subtropical western Australia (27°) eastwards to Victoria.

## Introduction

Recent publications on Australian sphaeromatids have revised the Cassidininae (Bruce, 1994b), and documented new and poorly known genera of Sphaeromatinae and Dynameninae (Bruce, 1992, 1993, 1994a; Poore, 1994).

This contribution results from searches of the collections held by the Australian Museum, the Museum of Victoria, Queensland Museum and the South Australian Museum, specifically to locate previously undescribed Australian genera. Genera of the Sphaeromatinae are described here but do not include new genera that may result from the splitting up of larger genera such as *Cymodoce* Leach.

The following abbreviations are used: Australian Museum (AM), Museum of Tropical Queensland (MTQ), Museum of Victoria (NMV), South Australian Museum (SAM), Zoologisk Museum, University of Copenhagen, New South Wales (NSW), Queensland (Qld), South Australia (SA), Tasmania (Tas.), Victoria (Vic.), Western Australia (WA), body length (BL), immature (imm), plumose marginal setae (PMS), plumose setae (PS), simple marginal setae (SMS).

## *Benthosphaera* gen. nov.

*Type species. Benthosphaera arkoola* sp. nov., here designated.

*Diagnosis of male.* Body moderately vaulted, variably smooth or setose. Cephalon with distinct rostrum separating antennule bases. Pereonites 1–6 of about equal width, pereonite 7 narrower than (*B. arkoola* sp. nov., *B. reburra* sp. nov.) or as wide as pereonite 6 (*B. guaware* sp. nov.); coxae angled laterally, those of pereonites 2–4 or 2–6 (*B. guaware* sp. nov.) distally narrowed; all coxae with distinct suture, ventrally with complex interlocking ridge and groove system. Pleonite 1 entire, prominently visible; pleonites 2–4 indicated by 2 separate sutures; posterior margin of pleon with 2 prominent keys. Posterior margin of pleotelson arcuate, without foramen or distinct exit channel, emarginate, with slight ventral depression present.

Epistome anterior margin projecting, rounded or distally subtruncate; mesially constricted. Antennule peduncle articles 1 and 2 robust, article 3 slender; article 2 short, about 0.3 as long as article 1. Antenna peduncle with 5 articles, article 5 of which is longest. Mandible

incisor multi- or single cusped; left mandible with large tricuspid lacinia mobilis and spine row; molar process prominent, surface serrate or nodular, proximal margin with teeth. Maxillule with 12 nodular spines on lateral lobe, mesial lobe with 3 large and 1 short stout plumose spine with further 2 simple spines. Maxilla with all lobes spinose, some spines of which are smooth, others serrate. Maxilliped palp articles 2–4 with mesial lobes; endite distal margin with plumose spines.

Pereopods all ambulatory, posterior margins of ischium to propodus of pereopods 2–6 with setulose fringe; posterior margins of pereopods 2–6 with serrate spines and also attenuated plumose spines; pereopods 1 and 7 with prominently serrate spines; pereopods 1–7 dactylus without flattened scales on posterior margin, accessory unguis simple.

Penes paired present, not fused, about 6 times as long as basal width.

Pleopods 1–4 with PMS; pleopods 3–5 exopods with transverse suture. Pleopod 1 endopod triangular, with proximomesial point. Pleopod 2 appendix masculina sub-basal in position; apex acuminate, bent mesially; longer than endopod. Endopods of pleopods 3–5 with thickened ridges varying from very weak (*B. arkoola*) to obvious (*B. guaware*); lateral margin of exopods of pleopods 4 and 5 with SMS; pleopod 5 with 3 or 4 scale patches, 2 proximal to suture, and third apical patch (*B. guaware* with fourth subapical patch). Uropods anterolateral, rami flat, subequal in length; exopod apex acuminate.

*Female.* Mouthparts not metamorphosed; ovigerous females with 3 pairs of oostegites arising from the coxae 2–4, and meeting at midline; males and females otherwise similar.

*Distribution.* East of Tully, north-eastern Queensland to east of Babel I., Tasmania; 150–1117 m.

*Etymology.* The Greek *benthos* (deep sea, sea bottom) and *-sphaera* (for the family) (feminine).

*Remarks.* There exists a group of sphaeromatine genera characterised primarily by having the posterior margin of the pleotelson flat, ventrally thickened, arcuate, and lacking a clear exit channel or groove. These genera lack developed cephalic or pereonal ornamentation, and pleotelson ornamentation is weak or absent. All have lamellar uropods, with only *Neosphaeroma* having the exopod conspicuously shorter than the exopod. Diagnoses have recently been given by Harrison and Holdich (1984) and Jacobs (1987) but the diagnoses are not compatible and the characters that separate these genera are few. Their principle distinguishing characters can be summarised, without referring to character polarisation, as follows.

*Exosphaeroides* Holdich and Harrison, 1983. Pleopods 4 and 5 thickened, without ridges or folds; female with 2 pairs of oostegites. Otherwise as for *Exosphaeroma*.

*Exosphaeroma* Stebbing, 1900. There is no recent detailed diagnosis for this genus, although it too was rediagnosed against *Sphaeroma* and *Lekansphaera* by Jacobs (1987). Characters here are derived from Jacob (1987) and Brandt and Wägele (1989). Pleopods 1–3 lamellar, pleopods 4 and 5 endopods usually with thickened ridges. Uropod rami flat and simple; maxilliped palp articles 2–4 with mesial lobes; pereopods without stiff setae, pereopods 4–7 subsimilar; penes short.

*Lekansphaera* Verhoeff, 1943. Pleopods 1–3 lamellar, pleopods 4 and 5 endopods with thickened ridges. Uropod exopod lanceolate, apically acute, lateral margin smooth or variably serrate; maxilliped palp articles 2–4 with mesial lobes; pereopods 1–3 with stiff setae on anterior margins of ischium and merus, pereopods 4–7 subsimilar; penes short.

*Neosphaeroma* Baker, 1926. Pleopods 1–2 lamellar, pleopods 3–5 endopods with thickened ridges. Uropod exopod short, lateral margin excised; maxilliped palp articles 2–4 with mesial lobes; pereopods 1–3 without stiff setae, pereopods 4–7 subsimilar; penes long.

*Sphaeroma* Bosc, 1802. Pleopods 1–3 lamellar, pleopods 4 and 5 endopods with thickened ridges. Uropod exopod lanceolate, apically acute, lateral margin obviously serrate; maxilliped palp articles 2–4 without mesial lobes; pereopods 1–3 with stiff setae on anterior margins of ischium and merus, pereopods 4 and 5 shorter and more robust than 6 and 7; penes short.

It can be seen that the important distinguishing characters are to be found the morphology of uropods, maxilliped palp, pereopods and pleopods. Although pleopod ridges may be secondarily lost (as in *Cymodocella* Pfeffer, 1887, Dynameninae, see Brandt and Wägele, 1989), their presence and arrangement is significant. Differences shown in uropod morphology are also regarded as of generic significance.

*Benthosphaera* gen. nov., *Neosphaeroma* Baker, 1926 and *Caecocassidias* Kussakin, 1967 are the only sphaeromatid genera known to have thickened ridges on the endopod of pleopod 3 (Harrison and Holdich, 1984). *Neosphaeroma*, while being readily distinguished by the short excised uropodal exopod, anteriorly acute epistome which does not project, and an evenly rounded or subtruncate pleotelson posterior margin, is otherwise similar. *Neosphaeroma* currently has only two species (Harrison and Holdich, 1984), and I am aware of at least one further species, and all of these species lack dorsal setae; three of the four species of *Benthosphaera* have setose dorsal surfaces. *Caecocassidias*, distinguished its hugely expanded cephalon, otherwise bears little resemblance to *Benthosphaera*. Other characters typical of *Benthosphaera* are the presence of slender recurved plumose spines on the posterior margin of the pereopods and the maxillule mesial lobe with one short and three long spines.

As revisionary studies of the Sphaeromatidae continue, it has become apparent that in several genera (e.g., *Exosphaeroma*, *Cymodocella* Pfeffer, 1887, *Cymodoce* Leach, 1818) the characteristic ridges or folds of pleopods 4 and 5 or 3–5 may be reduced or absent in one or more species. In the case of *Benthosphaera arkoola*, it results in the species keying to *Exosphaeroma* in Harrison and Ellis (1991). *Exosphaeroma* is a large genus with about 40 species ascribed to it but Harrison and Ellis (1991: 939) allowed only four as belonging with certainty. *Exosphaeroma* ("sensu strictu", description given by Brandt and Wägele, 1989) can be separated from *Benthosphaera* by pleonite 1 having two posteriorly directed submedian flat lobes (see Menzies, 1962: figs 43B, C) (versus *Benthosphaera* with pleonite 1 without lobes), by lacking dorsal setae (versus with setae), the coxae being ventrally directed (versus laterally directed), the appendix masculina being simple (versus acuminate, narrowed, with apex bent), and the uropod exopod is simple (versus apically falcate).

Sphaeromatidae are poorly represented beyond the continental shelf, Harrison and Ellis (1991) listing only six genera with representatives at depths greater than 400 m (Table 1). One of these, *Cassidina*, probably does not occur

Table 1. Sphaeromatidae recorded from depths of 400 m and greater.

| Species | Location | Depth (m) | Reference |
|---|---|---|---|
| *Benthosphaera arkoola* sp. nov. | eastern Australia | 150–400 | present report |
| *Benthosphaera guaware* sp. nov. | northeastern Australia | 1117 | present report |
| *Benthosphaera reburra* sp. nov. | northeastern Australia | 458–500 | present report |
| *Caecocassidias patagonica* | off Argentina | 400–680 | Kussakin, 1967 |
| *Ceratocephalus grayanus* | southeastern Australia | 32–498 | Bruce, 1994a |
| *Cymodoce acanthiger* | South Africa | 600 | Barnard, 1914 |
| *Cymodoce africana* | South Africa | 160–600 | Barnard, 1914 |
| *Cymodoce allegra* | off New Zealand | 0–615 | Hurley and Jansen, 1977 |
| *Cymodoce australis* | New Zealand | 0–611 | Hurley and Jansen, 1977 |
| *Cymodoce japonica* | Japan | 1547 | Harrison and Holdich, 1984 |
| *Cymodopsis impudica* | New Zealand | 425–1225 | Hurley and Jansen, 1977 |
| *Cymodopsis sphyracephalata* | off New Zealand | 611 | Hurley and Jansen, 1977 |
| *Cymodopsis torminosa* | off New Zealand | 549–1225 | Hurley and Jansen, 1977 |
| *Dynameniscus carinata* | western Atlantic | 804–1033 | Richardson, 1905 |
| *Moruloidea darwini* | off Argentina | 70–700 | Kussakin, 1967 |
| *Naesicopea abyssorum* | Indonesia | 1957 | Beddard, 1886; Stebbing, 1893 |
| *Paracassidina anasilla* | southeastern Australia | 32–466 | Bruce, 1994b |
| *Parasphaeroma prominens* | South Africa | 300–460 | Stebbing, 1902 |
| *Waiteolana tuberculata* | off Argentina | 400–500 | Kussakin, 1967 |

beyond about 100 m (Bruce, 1994b), while *Cymodoce japonica* Richardson, 1906 has been recorded from the continental slope at 1547 m (Harrison and Holdich, 1984). Records of other *Cymodoce* species from deep localities are of species that probably do not belong to that genus, and none exceeds about 600 m. The records for *Caecocassidias* Kussakin, 1967, *Dynameniscus* Richardson, 1905, *Waiteolana* Baker, 1926, *Naesicopea* Stebbing, 1893, and *Cymodopsis* Baker, 1926 (Hurley and Jansen, 1977) are all reliable. Thus *Benthosphaera* is one of only four sphaeromatid genera that are primarily slope-dwelling and *Benthosphaera guaware* is only the sixth species of sphaeromatid to be recorded from beyond 1000 m.

**Key to species of *Benthosphaera***

1. Dorsal surfaces smooth, without setae; pleotelson posteriorly acute; uropod endopod posteriorly truncate ..... *B. guaware*

— Dorsal surface with varying degrees and arrangements of setae; pleotelson posteriorly rounded or subtruncate; uropod endopod posteriorly rounded or falcate ..... 2

2. Dorsal surfaces covered by mass of setae; pereonite 7 only slightly narrower than 6; uropod rami extending beyond posterior of pleotelson .. *B. reburra*

— Dorsal surfaces with setal tufts or fine pilosity; pereonite 7 distinctly narrower than 6; uropod rami not extending to posterior margin of pleotelson ... 3

3. Dorsal surfaces with tufts of setae; coxae splayed laterally; posterior margin of pleotelson with shallow notch ..... *B. arkoola*

— Dorsal surfaces with fine pilosity; coxae weakly extended laterally; posterior margin of pleotelson without notch ..... *B.* sp.

***Benthosphaera arkoola*** sp. nov.

Figures 1–5

*Material examined.* Holotype. Vic, south of Point Hicks (38°17.7′S, 149°11.3′E) 24 Jul 1986, 400 m, coarse sand, gravel, mud, many sponges, M.F. Gomon et al., NMV J36939 (♂ 5.2 mm).

Paratypes. Same data as holotype: NMV J19162 (2 specimens), ZMUC CRU167 (♂ 5.0, dissected, 3 slides; imm. 4.5 mm; 7 ♀ ovig. 5.7, 5.2, 4.0, 3.7 mm, non-ovig. 5.7, 5.4, 5.0 mm; 9 sex indeterminate 4.3–3.7 mm; 26 mancas 2.0–3.0 mm). NSW, east of Eden (37°06S, 150°20.7E) 21 Jul 1986, 363 m, coarse shell, G.C.B. Poore et al., NMV J19161 (♂ 5.2 mm, 4 mancas). Tas, 50 km northeast of Babel I. (30°40.3S, 148°46.5E) 27 Mar 1979, 293 m, rock, coarse sand, G.C.B. Poore, NMV J26304 (♂ 5.8 mm, ♀ ovig. 5.4 mm).

Other Material. Qld, east of Lady Elliot I. (24°03.7′S, 152°49.4′E) 4 Jun 1984, 150 m, rubble and solitary corals, P. Colman, S. Keable and G. Hangay, AM P42560 (♂ 4.9 mm).

*Description of male.* Body about 1.7 times as long as wide, dorsum smooth, with tufts of setae on coxae, pereonite lateral margins, cephalon and pleotelson; widest at pereonite 5; pereonite 7 narrower than 6, not extending to lateral body margin. Cephalon with single anteromedian tubercle; and obscure low transverse ridge posteriorly; eyes lateral, round, facets distinct. Pereonite 1 longer (1.2 in lateral view) than pereonite 2, pereonites 2–6 subequal in length, 7 slightly shorter than 6; coxae of pereonites 2–3 distally narrowed.

Antennule peduncle article 2 longest, about 3 times as long as article 2 and about 2.2 as long as article 3; flagellum of 8 articles, about 0.7 times as long as peduncle, extending to pereonite 2; peduncle article 1 with numerous plumose setae, and anterodistal margin with distinct ridge. Antenna flagellum with 10 articles, subequal in length to peduncle. Mandible with prominent molar and multicusped incisor; left mandible with prominent 3-cuspid lacinia mobilis, spine row of 8 spines; right mandible with lacinoid spine and spine row of 7 spines; palp with 5 biserrate setae on distomesial margin of article 2, 16 biserrate setae on mesial margin of article 3, distal 2 of which are longest. Maxilla lateral lobe with 4 finely serrate setae; middle lobe with 6 prominently serrate setae; mesial lobe with dense mass of smooth and plumose spines. Maxillule lateral lobe with 12 stout nodular spines and 1 slender articulating spine on gnathal surface; mesial lobe with 2 short simple spines in

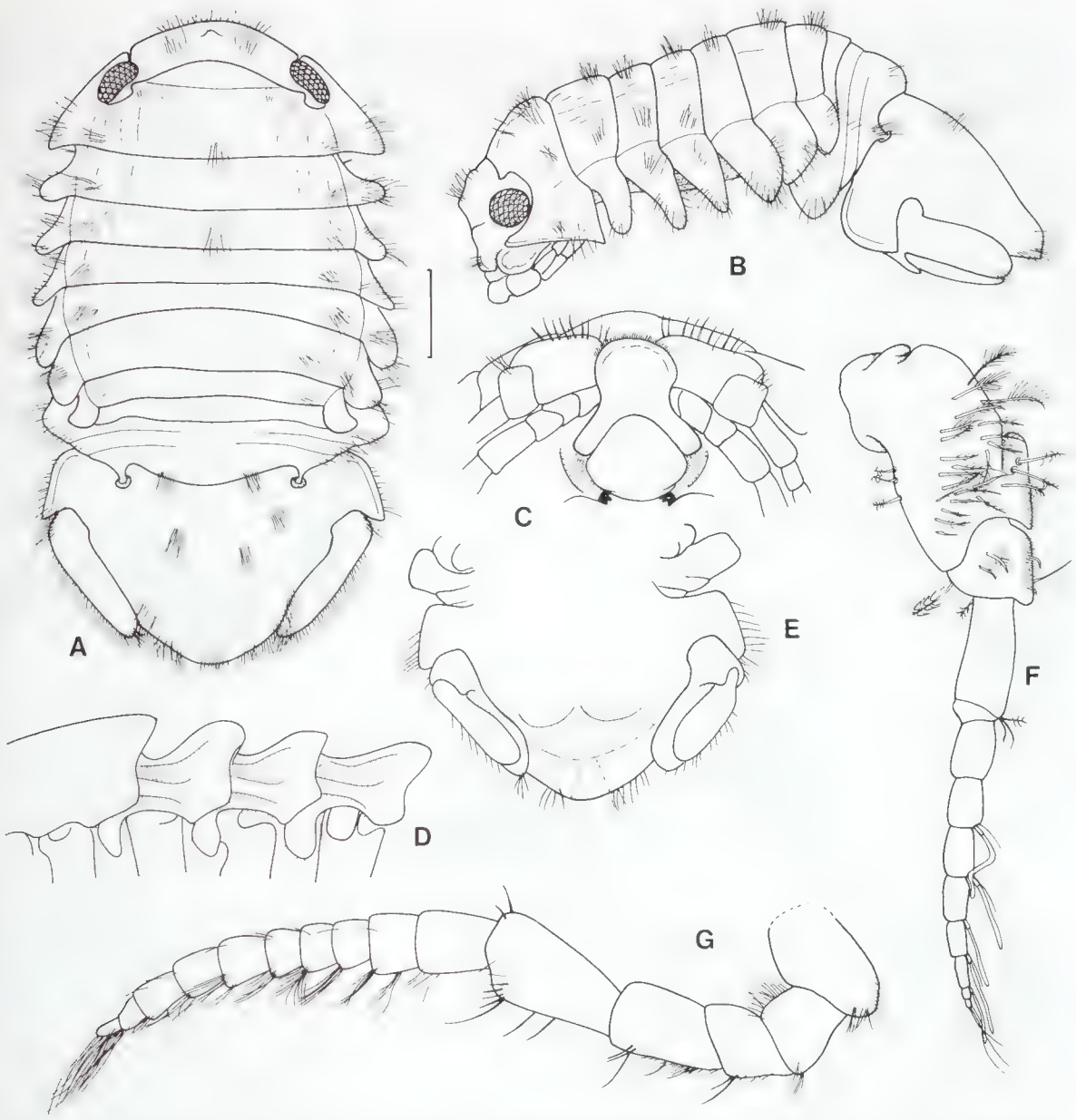


Figure 1. *Benthosphaera arkoola* sp. nov. Figs A–E holotype, remainder ♂ 5.0 mm, NMV J19162. A, dorsal view; B, lateral view; C, frons; D, pleonites 2–4, ventral aspect; E, pleotelson, posterior margin, in ventral view; F, antennule; G, antenna. Scale 1.0 mm.

addition to 4 major spines. Maxilliped palp articles 2–5 with about 7, 9, 10, and 12 setae respectively; endite distal margin with single row of 6 plumose spines, and single stout simple spine at mesiodistal angle; dorsal distomesial margin with 3 plumose spines.

Pereopod 1 shorter than 2, pereopods 2–5 and 7 shorter than 6; pereopods 1–3 with setulose fringe on posterior margins of merus and carpus, weak setulose fringe on ischium and propodus; pereopods 6 and 7 with weak setulose fringe on basis and ischium. Pereopod 1 with stout acute spines on posterior margins of merus, carpus and propodus; spines on pereopods 2 and 3 slender. Pereopod 6 with serrate and plumose spines on posterior margin of merus and carpus, serrate


Figure 2. *Benthosphaera arkoola* sp. nov. All figs ♂ 5.0 mm, NMV J19162. A, left mandible; B, right mandible, apex; C, left mandible, apex; D, maxillule; E, maxillule, lateral lobe detail; F, maxillule, medial lobe detail; G, maxilla; H, maxilliped; I, penes.

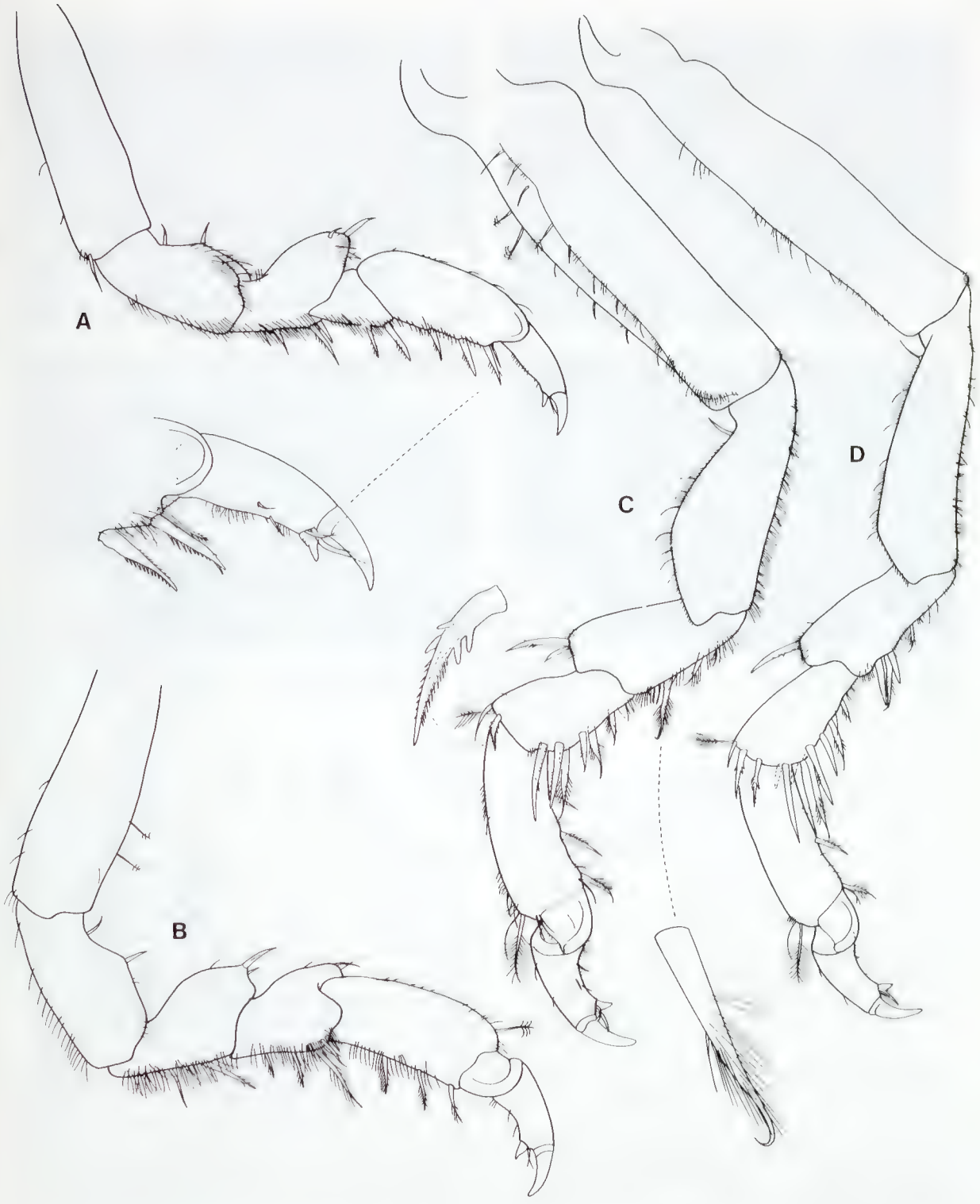


Figure 3. *Benthosphaera arkoola* sp. nov. All figs ♂ 5.0 mm, NMV J19162. A–D, pereopods 1, 2, 6, 7, respectively.


Figure 4. *Benthosphaera arkoola* sp. nov. All figs ♂ 5.0 mm, NMV J19162. A–E, pleopods 1–5, respectively; F, uropod.

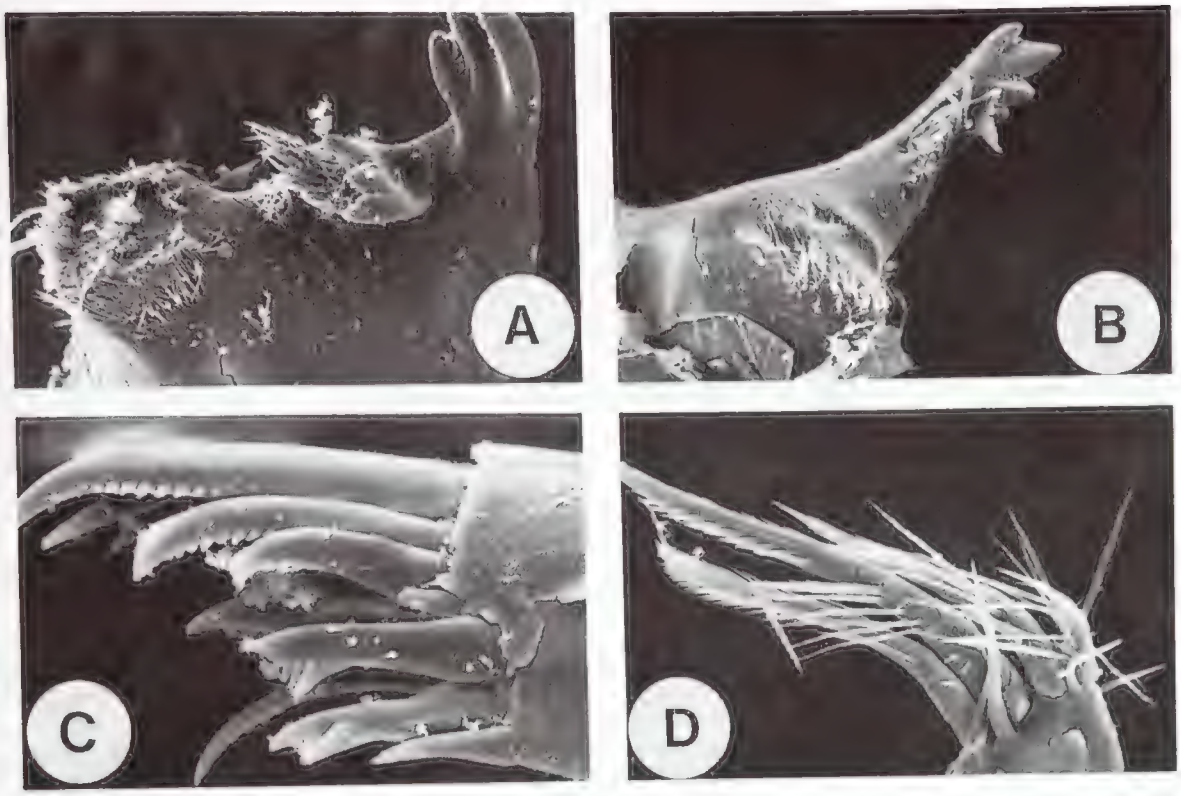


Figure 5. *Benthosphaera arkoola* sp. nov. SEMs. A, left mandible (430 ×); B, right mandible (350 ×); C, maxillule, lateral lobe (1200 ×); D, maxillule, medial lobe (1000 ×).

spines only on anterior margin. Pereopod 7 with elongate spines on distal and posterior margin of merus.

Penes elongate, about 5 times as long as basal width; apically folded over.

Pleopod 1 with about 20 and 27 PMS on endopod and exopod respectively; exopod with prominent simple spine present at proximolateral angle. Pleopod 2 endopod and exopod with about 32 and 30 PMS respectively; appendix masculina about 1.3 times as long as endopod, abruptly narrowing just beyond point of endopod distal margin to form distinct elongate narrowed tip, 0.26 of total length. Pleopod 3 endopod and exopod with 17 and 28 PMS respectively; endopod with extremely faint thickenings scarcely visible. Pleopod 4 endopod and exopod with 4 and 6 PMS respectively on distal margin only, faint ridges visible on endopod. Pleopod 5 with faint ridges visible. Uropod endopod about 2.5 times as long as greatest width, distally bluntly rounded; exopod about 0.7 times as long as endopod, distally narrowed with laterally angled acuminate apex; both rami with abundant PS on dorsolateral surfaces, particularly dense on distolateral surface of endopod.

*Female.* Similar to male, oostegites on coxae 2–4.

*Colour.* All specimens are pale cream to white, without evident chromatophore pattern.

*Size.* Males 5.0–5.8 mm, one immature male measured 4.5 mm; ovigerous females 3.7–5.7 mm, non-ovigerous females 5.0–5.7 mm; mancas 2.0–3.0 mm.

*Distribution.* Eastern Australia from off Lady Elliot I., southern Great Barrier Reef to off Tasmania; 150–400 m.

*Etymology.* An Aboriginal word meaning hair (noun in apposition).

*Remarks.* This species, the only one of the genus known from more than one specimen, is readily recognized by the tufted setae over the dorsal surfaces, and the narrow pereonite 7 which does not form part of the lateral body margin. *Benthosphaera reburra* is densely covered by setae,

and has the uropods extending beyond the posterior margin of the pleotelson, while the very much larger *B. guaware* is devoid of dorsal setae, has an anteriorly subacute epistome, and a truncate uropodal endopod (and many other differences). The most similar species is the undescribed *Benthosphaera* sp. (see below).

### ***Benthosphaera reburra*** sp. nov.

Figures 6, 7

*Material examined.* Holotype. Qld, east of Innisfail (17°35′S, 146°53′E) 15 May 1986, 458–500 m, sledge, M. Pichon, P. Arnold and A. Birtles on R.V. *Cidaris*, MTQ W13595 (♂ 8.4 mm).

*Description of holotype.* Body about 1.5 times as long as wide; exposed dorsal surfaces entirely covered by dense mass of setae; widest at pereonite 6, pereonite 7 not extending to lateral body margins.

Antennule peduncle articles 1 and 2 anteriorly finely nodulose; flagellum of 10 articles, extending to posterior of pereonite 1. Antenna flagellum of 13 articles, extending to pereonite 3. Epistome anteriorly rounded, with fine nodules. Mouthparts generally similar to generic diagnosis and those of type species; maxilliped palp articles 2–5 with about 16, 16, 20 and 20 setae respectively.

Pereopod 1 with 5, 4 and 6 stout acute spines on posterior margin of merus, carpus and propodus respectively; ischium, merus and carpus with indistinct setulose fringe. Pereopods 2–7 distinctly more slender than 1, all with distinct setulose fringe on merus, carpus and propodus, with slender plumose spines set amid setules; additional stout acute spines present on distal margin of carpus of pereopods 6 and 7.

Pleopod 1 endopod and exopod with about 34 and 50 PMS respectively; ventral surface of exopod with scattered short simple setae. Pleopod 2 endopod and exopod with about 40 and 50 PMS respectively; appendix masculina narrowing at point just short of distal margin of endopod, about 1.3 times as long as endopod, narrowed apex, 0.28 of total length. Pleopods 3–5 all damaged; weak folds visible on endopod of pleopod 3, distinct on pleopod 5.

Uropod rami extending to or just beyond posterior margin of pleotelson; exopod with falcate acute apex.

*Colour.* White, chromatophores not apparent.

*Distribution.* Known only from the type locality.

*Etymology.* The Latin word *reburrus*, meaning one with bristling hair.

*Remarks.* This species is immediately recognized by the dense mass of setae that covers all the exposed dorsal surfaces. Additionally the uropods extend to the posterior of the pleotelson in contrast to the other species in which the uropods fall short of the posterior margin of the pleotelson.

### ***Benthosphaera guaware*** sp. nov.

Figures 8–11

*Material examined.* Holotype. Qld, east of Tully (18°08′S, 148°15′E) 7 May 1986, 1117 m, trawled, R.V. *Cidaris*, MTQ W13395 (♂ 18.5 mm).

*Description of holotype.* Body about 1.6 times as long as wide, dorsally smooth, unornamented; coxae of pereonites 2–5 strongly narrowed and splayed laterally; lateral margin of pereonite 1 and coxae 2–6 with sparse setae and small tubercles; widest at pereonite 6; pereonite 7 extending to lateral body margin. Pleotelson posteriorly acute.

Antennule and antenna as for genus; antennule peduncle articles 1 and 2 with scattered small nodules. Epistome anteriorly subtruncate, anterior portion granular. Mouthparts similar to type species except for: maxillule lateral lobe spines less nodulose, mesial lobe spines more densely serrate; maxilliped palp articles 2–5 with some stout marginal setae not distally tapered.

Pereopod 1 stout, robust; pereopods 2–7 with extremely dense ("fur-like") setulose fringe which largely conceals spination; pereopod 7 with stout acute spines on posterior margin of merus and carpus, and distal margin of carpus.

Pleopod 1 endopod and exopod with about 45 and 60 PMS respectively; mesial margin of endopod with recessed groove. Pleopod 2 endopod and exopod with about 38 and 60 PMS respectively; appendix masculina basally swollen, apex bent mesially, about 1.1 times as long as endopod, narrowed apex about 0.16 of total length. Pleopod 3 endopod and exopod with about 26 and 60 PMS respectively, endopod with distinct setule patch on mesial margin, with distinct thickened ridges. Pleopod 4 endopod and exopod with about 12 and 31 PMS respectively; endopod with distomesial setule; exopod with SMS on proximal lateral margin. Pleopod 5 with distinct thickened ridges on endopod, 2 distal and 2 medial scale patches.

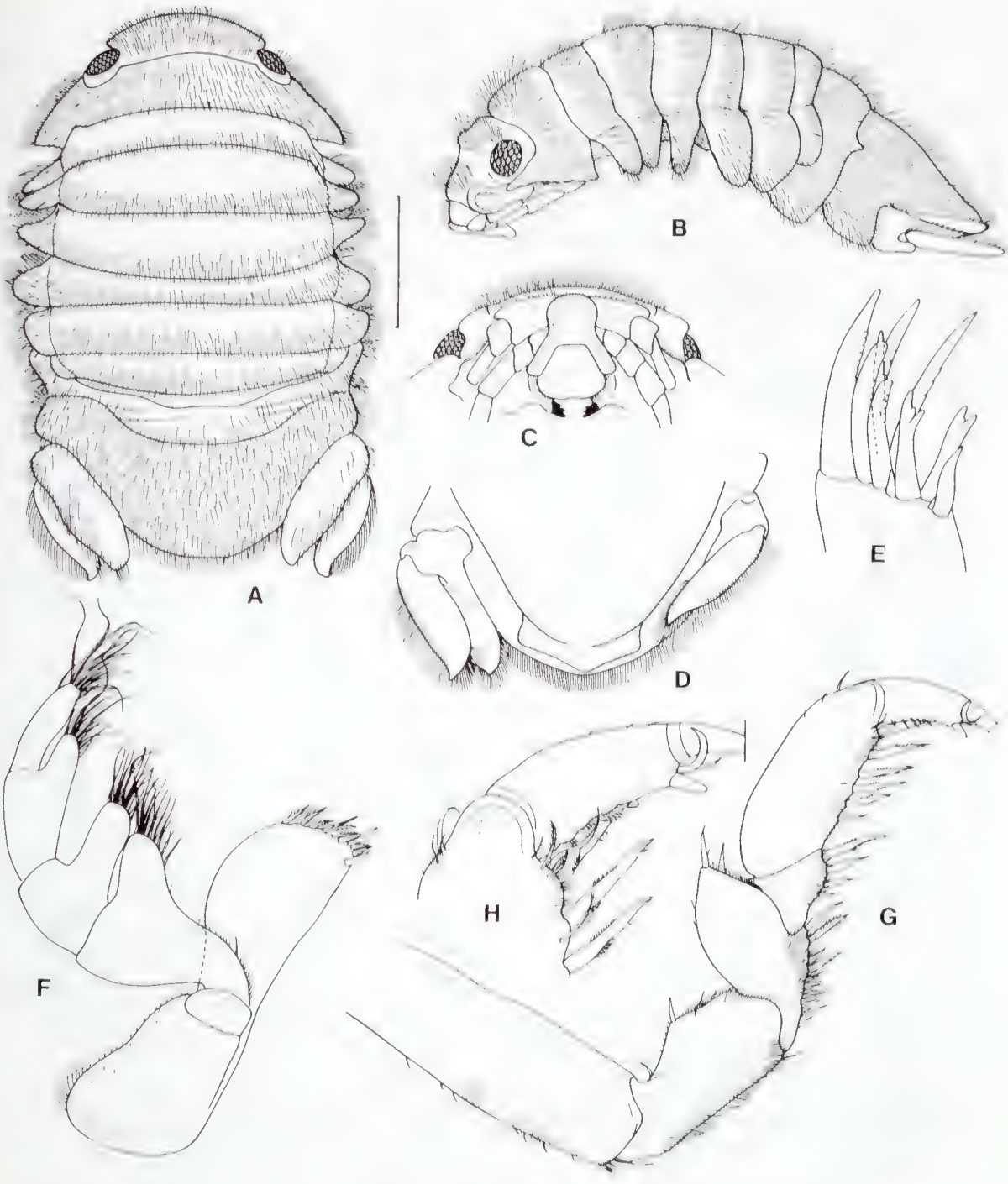


Figure 6. *Benthosphaera reburra* sp. nov., holotype. A, dorsal view; B, lateral view; C, frons; D, pleon, ventral view; E, maxillule, apex of lateral lobe; F, maxilliped; G, pereopod 1; H, pereopod 1 dactylus. Scale 2.0 mm.

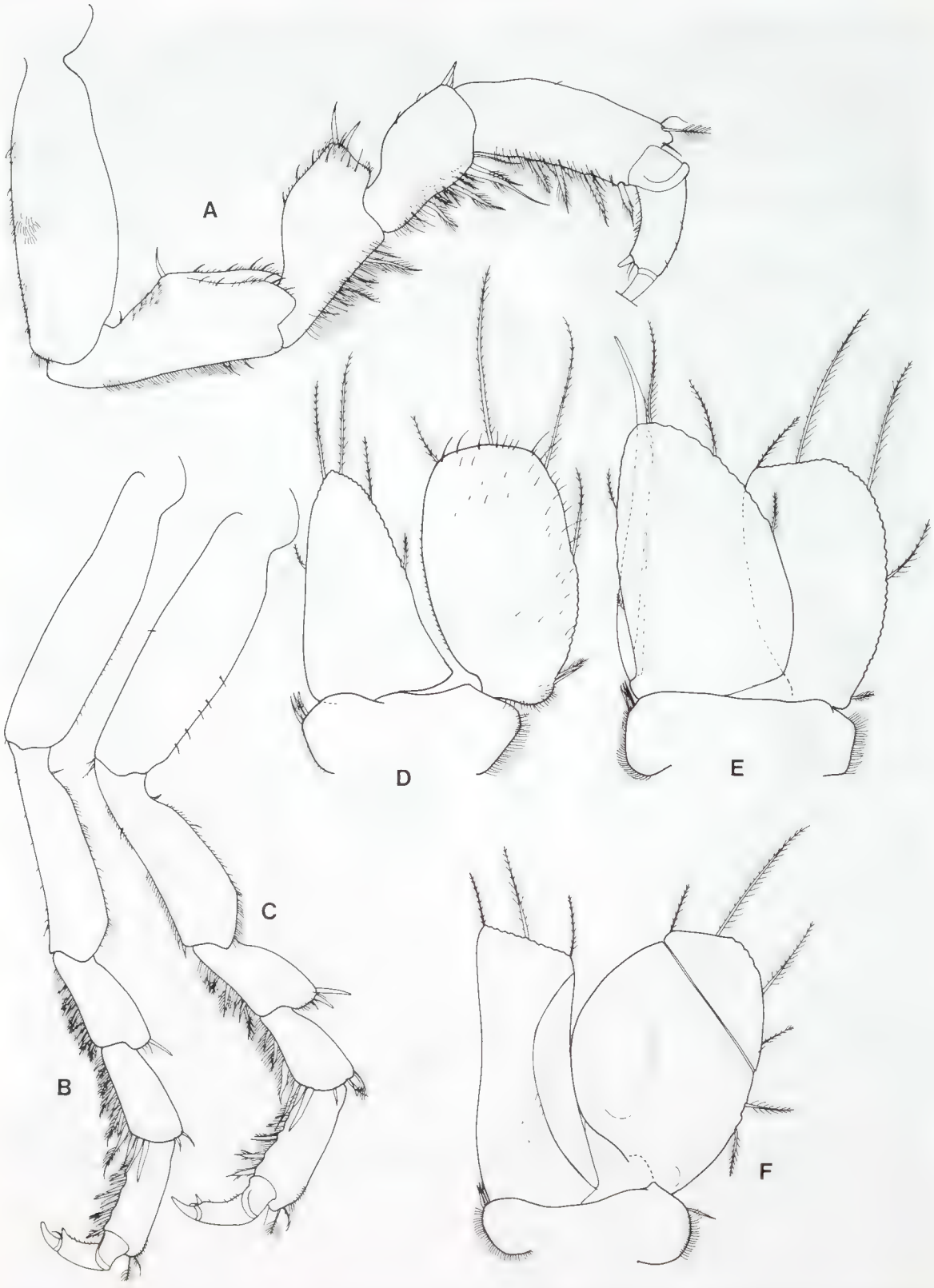


Figure 7. *Benthosphaera reburra* sp. nov., holotype. A, pereopod 2; B, pereopod 7; C, pereopod 6; D–F, pleopods 1–3 (pleopod 2 endopod folded over).

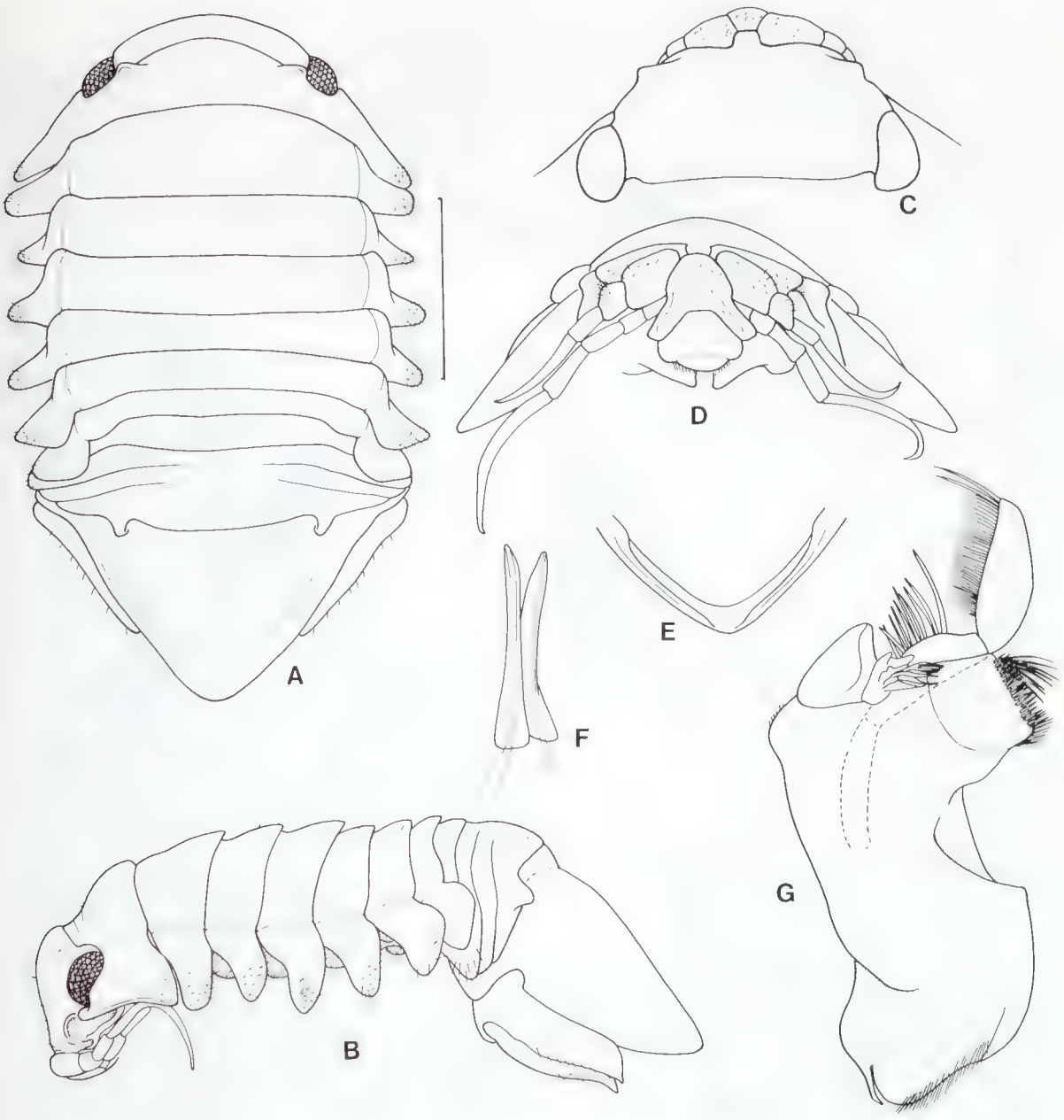


Figure 8. *Benthosphaera guaware* sp. nov., holotype. A, dorsal view; B, lateral view; C, cephalon, dorsal view; D, frons; E, ventral posterior margin of pleon; F, penes; G, mandible. Scale 5.0 mm.

Uropod endopod lateral margin weakly sinuate, apex subtruncate, indented; exopod apex bent laterally also subtruncate; neither ramus extending to posterior margin of pleotelson.

*Colour.* Pale tan, chromatophores not apparent.

*Distribution.* Known only from the type locality.

*Etymology.* An Aboriginal word meaning deep (noun in apposition).

*Remarks. Benthosphaera guaware*, at nearly 2 cm, is a large sphaeromatid, and is one of few sphaeromatids collected beyond a depth of 1000 metres (Table 1). Its large size, smooth dorsum, acute pleotelson, strongly splayed coxae distinguish it from its congeners.

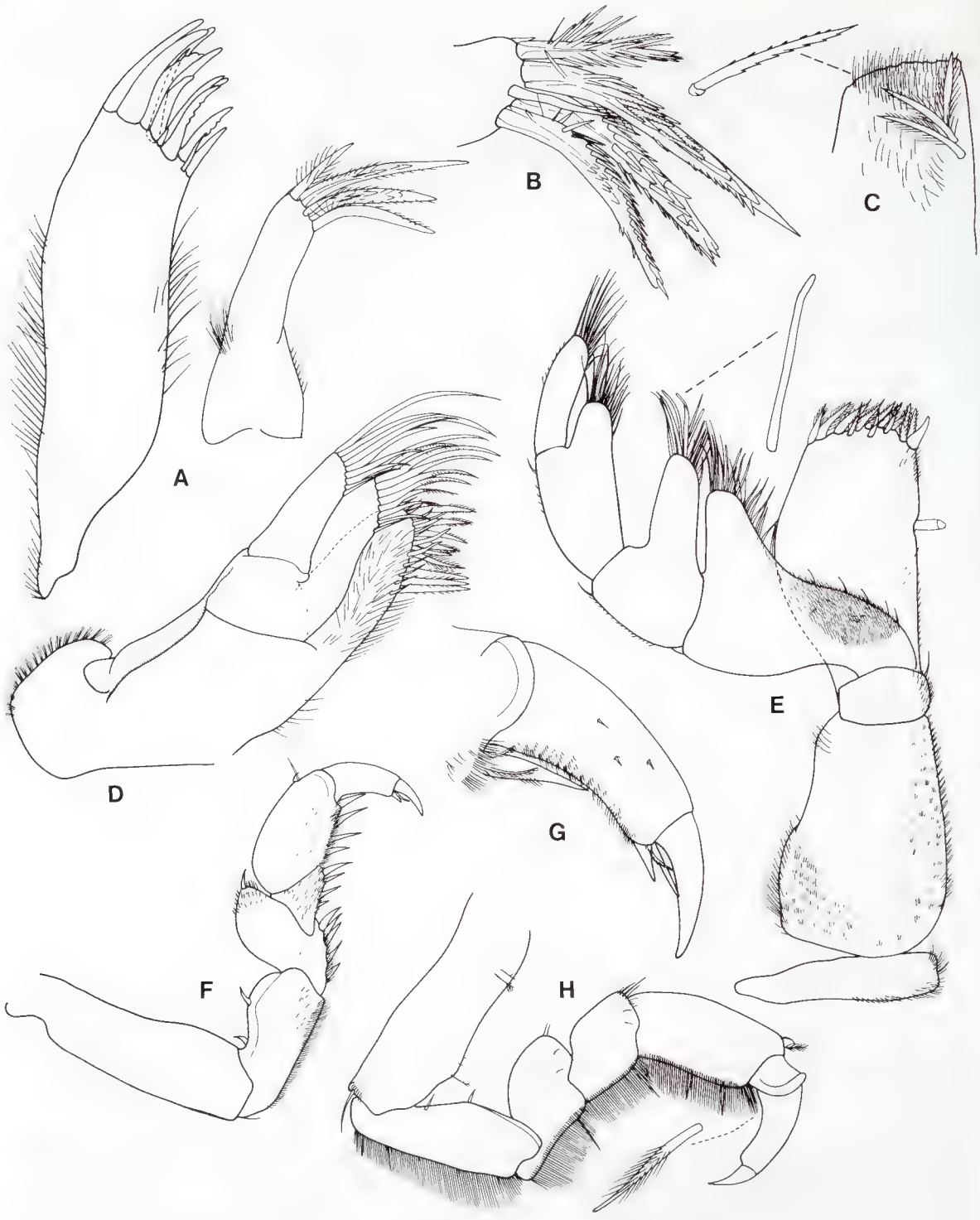


Figure 9. *Benthosphaera guaware* sp. nov., holotype. A, maxillule; B, maxillule, medial lobe; C, maxilliped endite, dorsal surface; D, maxilla; E, maxilliped; F, pereopod 1; G, pereopod 1, dactylus; H, pereopod 2.

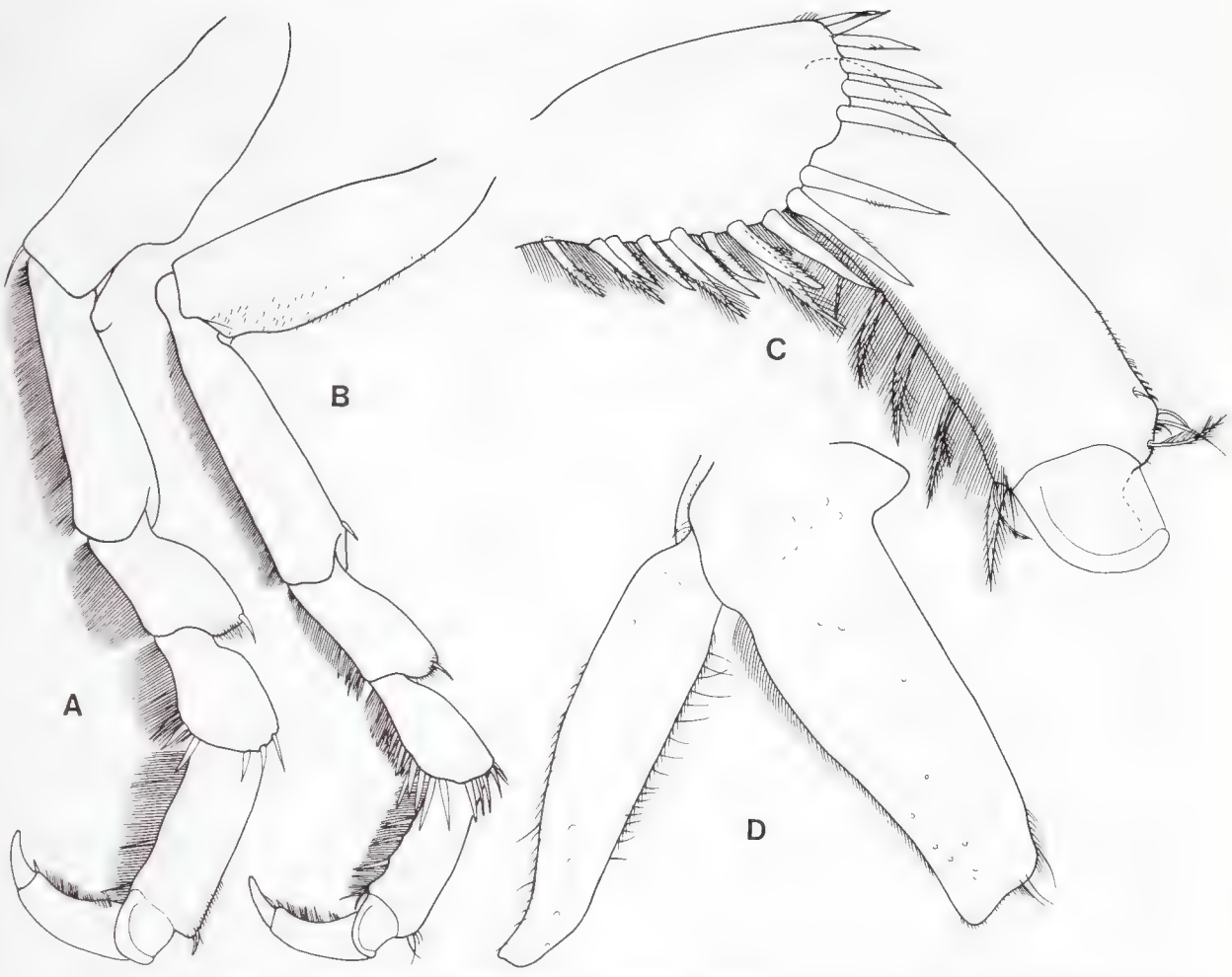


Figure 10. *Benthosphaera guaware* sp. nov., holotype. A, pereopod 6; B, pereopod 7; C, pereopod 7, distal carpus, propodus; D, uropod, *in situ*.

### ***Benthosphaera*** sp.

*Material examined.* NSW, off Port Hacking (34°11.1′S, 151°26.0′E) 5 Oct 1982, 198 m, W. Ponder and R.T. Springthorpe on R.V. *Tangaroa*, AM P42561 (♀ non-ovig. 3.6 mm).

*Remarks.* This single specimen, which was taken within the distributional range of *B. arkoola*, differs in several characters from it. It lacks dorsal tufts of setae, having instead a fine pilosity, the posterior margin of the pleotelson is narrower and lacks any trace of a ventral notch, antennule peduncle articles 1 and 2 are relatively longer, and the coxae are angled more ventrally.

Dorsal setation on *Benthosphaera arkoola* varies, as does the prominence of the cephalic tubercle. It therefore seems prudent to draw attention to a fourth species in the genus, and so avoid its confusion with *B. arkoola*, but defer description until more material is available.

### ***Xynosphaera*** gen. nov.

*Type species. Xynosphaera colemani* sp. nov., here designated.

*Diagnosis of male.* Body strongly vaulted, smooth, without processes or cuticular ornamentation. Cephalon without distinct rostrum, but antennule bases separate; eyes large. Pereonites 2–6 subequal in length, pereonite 7 shorter (0.7) than 2–6; coxae each with distinct suture, distally subtruncate, not narrowed; coxae of pereonite 7 rounded. Pleonite 1 entire, largely concealed by pereonite 7, pleonites 2–4 indicated by 2 separate sutures running to posterior margin of

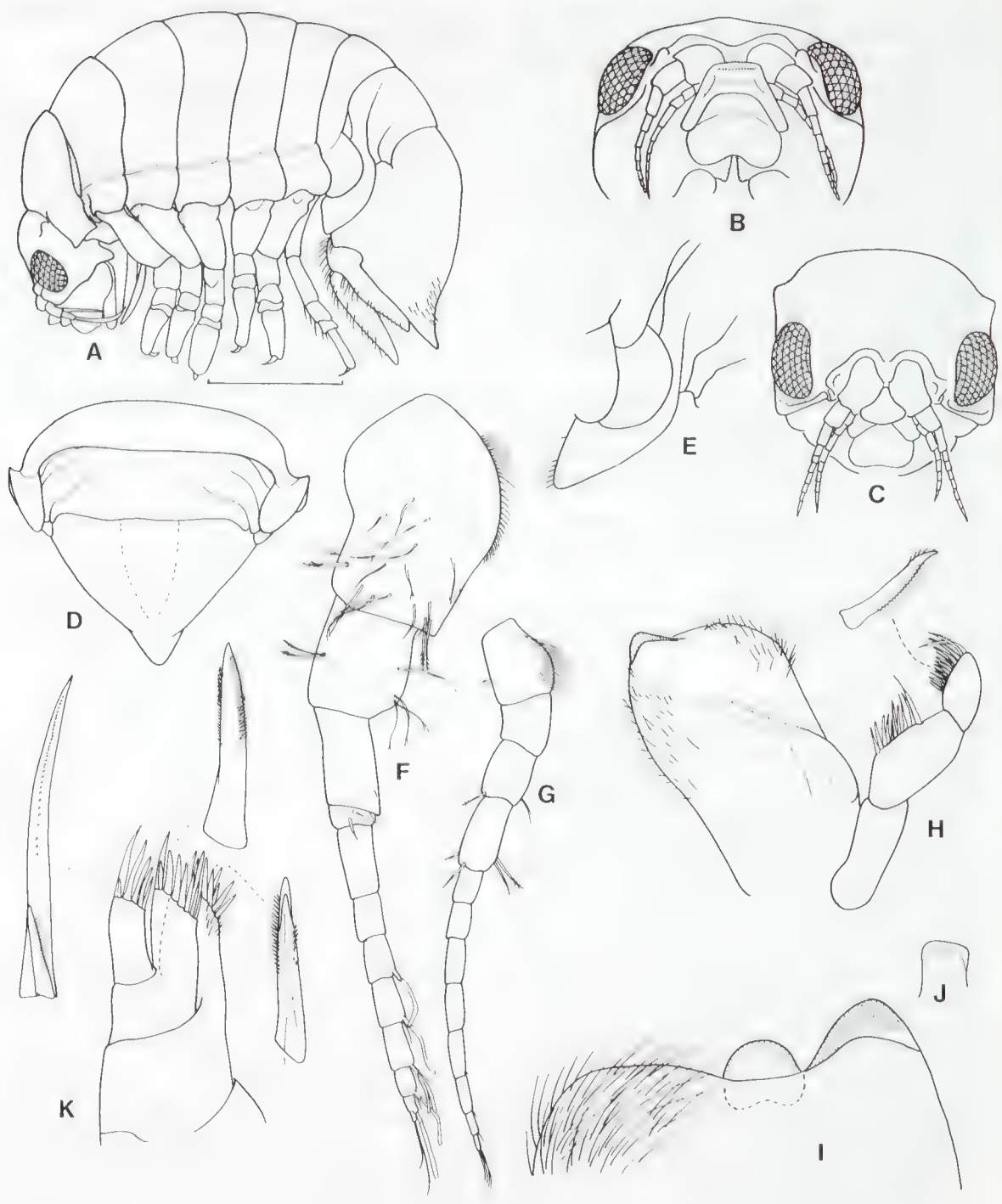


Figure 12. *Xynosphaera colemani* sp. nov. A, B and J, holotype, remainder paratype. A, lateral view; B, frons; C, cephalon, anterior view; D, pleon and pleotelson, dorsal view; E, pleon, lateral view, showing sutures; F, antenna; G, antennule; H, right mandible; I, left mandible, distal margin; J, mandible incisor, drawn *in situ*; K, maxillule. Scale 3.0 mm.

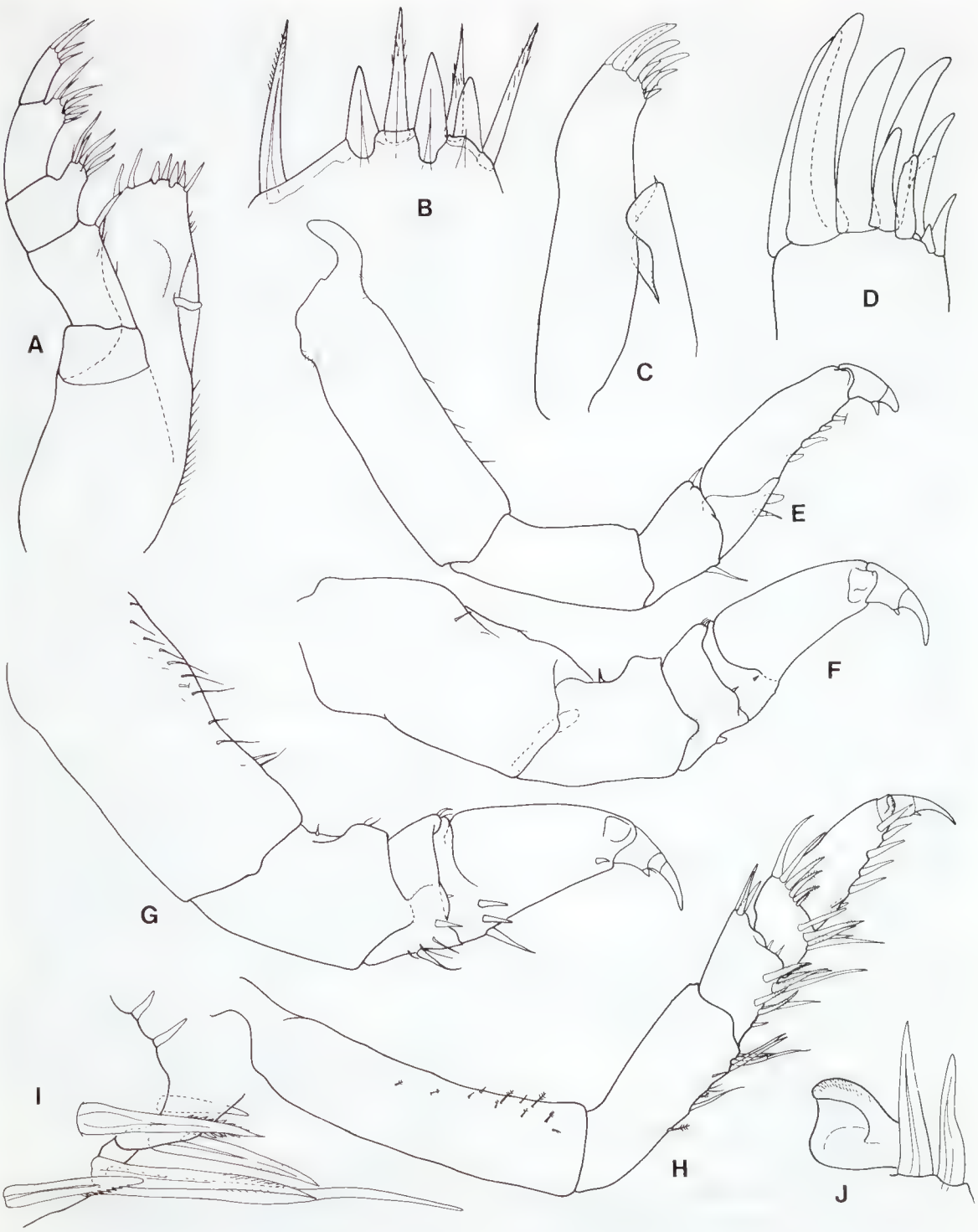


Figure 13. *Xynosphaera colemani* sp. nov. A–D, female paratype, remainder holotype. A, maxilliped; B, maxilliped endite, distal margin; C, maxillule; D, maxillule, lateral lobe; E–H, pereopods 1, 2, 6, 7, respectively; I, pereopod 7, merus posterior spines; J, pereopod 7, distal margin of propodus.

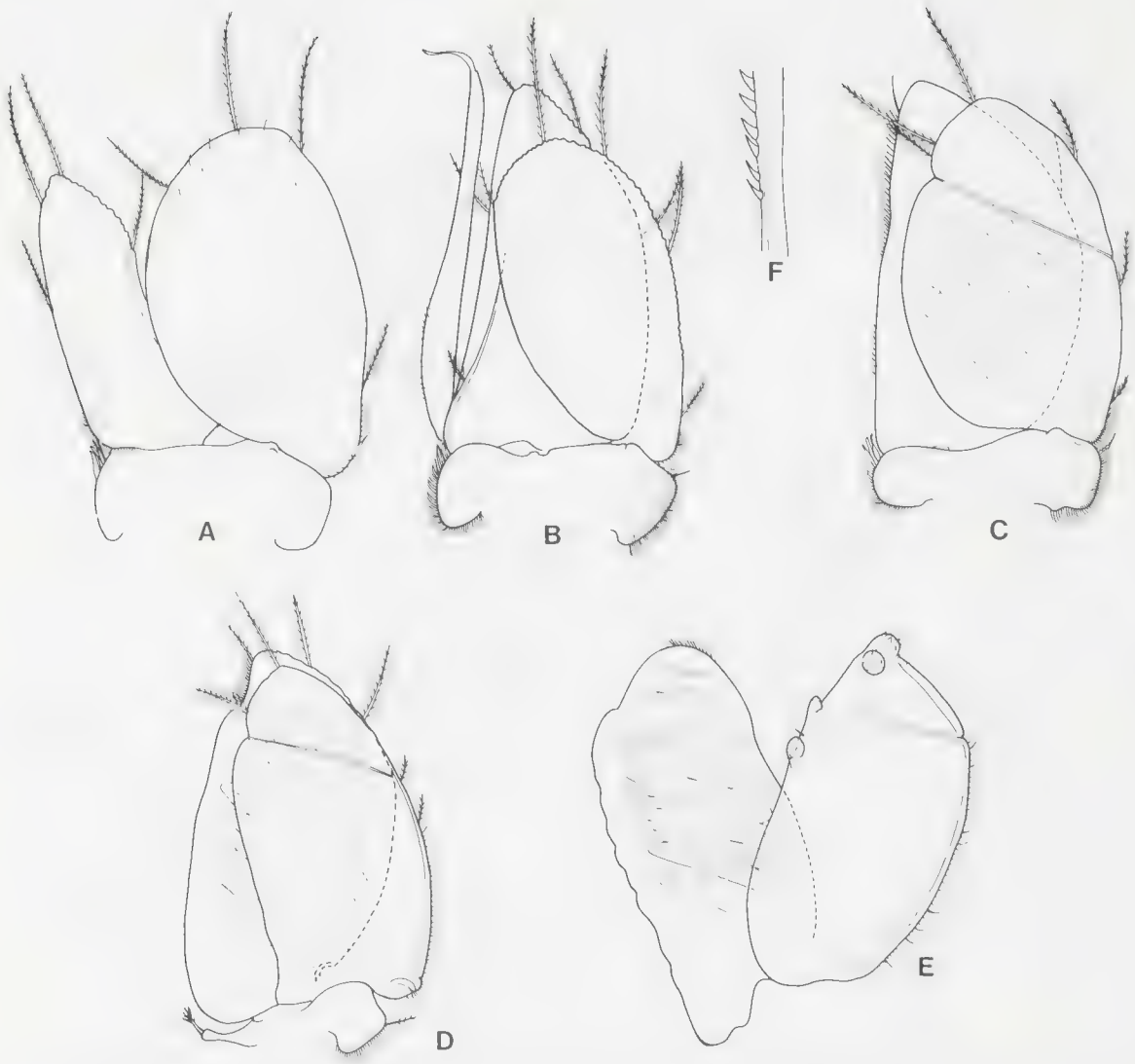


Figure 11. *Benthosphaera guaware* sp. nov., holotype. A–E, pleopods 1–5, respectively; F, pleopod 2 exopod, medial margin, showing scales.

pleon. Pleotelson posterior margin entire, without foramen or ventral exit channel; apex with prominent caudomedial point.

Antennule peduncle not flattened or otherwise expanded, articles 2 and 3 subequal in length. Antenna peduncle with 4 articles. Mandible robust, incisor a single truncate cusp in ventral view; lacinia mobilis single simple cusp on right mandible; spine row absent; molar reduced to simple setose swelling. Maxillule lateral lobe with 11 simple stout spines, mesial lobe reduced, without spines. Maxilla with all lobes with blade-like, finely serrate spines. Maxilliped palp articles 3 and 4 with mesial lobes; mesial margins of palp articles 3–5 with blade-like spines, article 2 with single spine; lateral margins without spines; endite with 3 simple and 4 serrate blade-like spines on distal margin.

Pereopods all robust, largely without setae, setules and cuticular scales. Pereopod 1 with stout dactylus, which has prominent simple accessory unguis and stout short acute spines on propodal palm and posterior margin of merus; pereopods 2–6 with few spines or setae, distal

scattered setules on ventral surface; endopod distally tapering, slightly longer than exopod, with about 27 PMS. Pleopod 2 exopod and endopod with about 60 and 27 PMS respectively; mesial margin of endopod with incipient appendix masculina. Pleopod 3 exopod and endopod with about 54 and 22 PMS respectively. Pleopod 4 without PMS, exopod with short SMS on proximal lateral margin. Pleopod 5 exopod with 3 scale patches, distal patch being large; proximal lateral margin short SMS. Uropod endopod straight, narrowing evenly to rounded apex, with finely serrate mesial margin; with abundant long SMS; exopod lateral margin strongly sinuate, apex narrow; lateral margin with abundant setae; exopod distinctly longer (1.6) than endopod.

*Female.* As for genus.

*Colour.* Photographs taken by Neville Coleman show the animal to be entirely creamy white, the eyes also being without pigment.

*Size.* Adults 11.5–13.3 mm.

*Distribution.* Philippines, northeastern Australia, northern Madagascar.

*Habitat.* The two adult specimens were collected by Neville Coleman, who "squeezed them from a small burrow with a slit-like aperture" on the stem of the alcyonarian. The alcyonarian has been identified, from colour photographs, as probably belonging to the family Nephthyidae (Alcyonacea).

*Etymology.* The epithet honours Mr Neville Coleman, photographer and collector of this unusual isopod.

*Remarks.* The rarity of collected specimens is almost entirely attributable to its cryptic way of life. It is readily identified by the generic characters, and cannot be confused with any other isopod.

### ***Bregmotypta*** gen. nov.

*Type species. Bregmotypta pavicula* sp. nov., here designated.

*Diagnosis of male.* Anterior of cephalon produced into a conical process; ventral rostral process present, separating antennules; eyes lateral, facets distinct. Pereonite 1 longest, about twice as long as pereonite 2; posterior margins of pereonites 1–7 with nodular ridge; coxae indistinct, sutures not visible; overlapping anterior to posterior. Pleon of 4 segments, with 2 separate sutures running to posterolateral margins; pleonite 1 present, visible in lateral view. Pleotelson prominently bidomed, apex indistinctly trilobed, with indistinct ventral exit channel.

Epistome short, laterally constricted, not separating antennule bases. Antennule peduncle article 1 robust, article 2 very short, article 3 slender; flagellum shorter than peduncle. Antenna peduncle slender, articles 4 and 5 longest, subequal in length; flagellum shorter than peduncle. Mandible incisor unicuspid; left mandible with lacinia mobilis, spine row absent, right mandible with spine row of 2 or 3 spines; both mandibles with prominent molar process with flat mesial face, not obviously ornamented or rugose. Maxillule lateral lobe with 10 unornamented spines, mesial lobe spines with clubbed spinulations. Maxilla with all lobes spinose, some spines simple, some serrate. Maxilliped palp articles 2–4 with medial lobes; endite distal margin with plumose spines.

Pereopod 1 robust, shorter than 2–7 which are subsimilar. Pereopod 1 posterior margin of merus, carpus and propodus with prominent, stout apically trifid spines. Pereopods 2–7 with setulose fringe on posterior margin of merus and carpus.

Penes elongate, basally in contact, not fused; apices acute, extending beyond pleopod 1 peduncle.

Pleopod 1 endopod triangular, mesial margin dorsally recessed, accomodating penial process, exopod oblique, distally subtruncate. Pleopod 2 appendix masculina basal in position, extending beyond distal margin of endopod. Pleopods 1–3 with PMS; pleopods 3–5 with entire transverse suture. Pleopod 4 exopod lateral margin with SMS, distal margin with 2 short PMS; proximomedial lobe present. Pleopod 5 exopod lateral margin with SMS; mesial margin with 2 proximal scaled lobes, distomesial margin entirely scaled, ventral surface with further prominent scaled lobe. Uropodal rami short, not reaching posterior margin of pleotelson; exopod small, subcylindrical, articulating laterally on endopod.

*Female.* Not known.

*Etymology.* The Greek words *bregma* (front of the head) and *typto* (beat, strike), in other words, head-banger (feminine).

*Remarks.* The unique characters that immediately serve to identify the genus are the strongly produced cephalon, bidomed pleotelson, pleotelson lacking a defined ventral exit channel or

margin of merus partly fused to propodus; pereopod 7 with long blade-like spines on posterior margins of ischium-propodus and distal margins of carpus and merus.

Paired penes present on posterior of sternite 7 in submedian position, not fused, about 4 times as long as basal width.

Pleopod 1 not operculate, not indurate. Pleopod 2 appendix masculina not observed. Pleopods 1–3 both rami with PMS; pleopods 3–5 exopods with transverse suture; pleopods 4 and 5 endopods with prominently thickened fleshy folds; exopod of pleopod 5 with 2 large scale patches. Uropod exopod longer than endopod, both rami prominently setose.

*Female.* Similar to the male. Mouthparts not metamorphosed. Brood pouch formed from oostegites arising from coxae 2–4, overlapping at midline and provided with stout supports.

*Distribution.* Recorded from north-eastern Australia (Great Barrier Reef) Madagascar and the Philippines.

*Etymology.* From the Greek *xynos*, a companion or partner, alluding to its symbiotic habitat (feminine).

*Remarks.* This genus can easily be recognised by its strongly humped appearance and smooth body surfaces, together with the shape of the pleotelson which has a prominent caudomedial point, and by the shape of the uropodal rami.

This is the only sphaeromatid genus that appears to be an obligate internal symbiont of a marine organism. Species of the "*Cymodoce tuberculosa* group" are frequently recorded from sponges, and some clearly burrow into the sponge tissue (personal observation), but these species are apparently also taken in free-living habitats, and show no special morphological features that could be recognised as adaptations to symbiosis. Known external commensals include *Waiteolana gibbera* Harrison, 1984 (on gorgonians), *Neosphaeroma australe* (Whitelegge) (see Harrison and Holdich, 1984, on black coral) and an undescribed species of *Neosphaeroma* (from crinoids).

*Xynosphaera*, which shows a strong superficial similarity in body shape to *Cartetolana* (Cirolanidae, see Bruce, 1986), shows several characters that can be recognized as adaptations to a symbiotic habit: lack of cuticular ornamentation, almost total lack of setules, setae and spines, and the spines that there are, are blade-like and serrate (though there are no hooked spines as in the fish parasitic isopod families Aegidae and Cymothoidae).

### *Xynosphaera colemani* sp. nov.

Figures 12–14

*Material examined.* Holotype. Qld, off Mrs Watson's Beach, Lizard I. (14°40′S, 145°28′E) Nov 1975, in burrow in green soft coral, 5 m, N. Coleman, AM P41871 (♂ 11.5 mm).

Paratypes. Collected with holotype, AM P25202 (♀ ovig. 13.3 mm). Philippines, Tubajon Bay, Dinigat (10°20N, 125°32E) 19 July 1951, intertidal coral reef, R.V. *Galathea*, ZMUC CRU165 (manca 5.8 mm).

Other material. Madagascar, Nosi-Bé, S of Ambariobé (13°24.4′S, 48°22.9′E), under intertidal rocks with sponges, alcyonarians, anemones etc, J. Rudloe, 15 Jan 1964 USNM (3 immature specimens, 3.1, 3.4, 4.0 mm).

*Description of holotype.* Cephalon anterior margin blunt. Epistome anteriorly truncate in ventral view, with anterior portion projecting between antennule bases in frontal view.

Antennule peduncle article 1 as long as combined lengths of articles 2–4, subequal in length to peduncle; flagellum with 10 articles, article 1 of which is longest. Antenna peduncle articles 1 and 4 subequal in length and longer than articles 2 and 3 which are also subequal in length; flagellum with 8 articles, slightly longer (1.2) than peduncle. Mandible palp article 2 with 10 setae, article 3 with about 12 plumose setae. Maxilla lateral lobe with 6 spines, middle with 8, and mesial with 10 spines. Maxilliped palp articles 2–5 with 1, 7, 7 and 4 spines respectively.

Pereopod 1 merus with one short spine at anterodistal angle, and one slender spine at posterodistal angle; merus with 2 spines on posterodistal margin; propodus with 4 stout acute spines on palm. Pereopods 2–6 subsimilar. Pereopod 2 with single spine on posterior margin merus, additional small spines on distolateral margin of merus and carpus; carpus distal margin fused with propodus. Pereopod 6 with sparse setae on anterior margin of basis; merus with 3 setae and 2 acute spines, carpus with 3 acute spines, propodus with small setae on palm, small spine on distolateral margin; carpus partly fused with propodus. Pereopod 7 more slender and longer than pereopods 2–6; posterior margins of ischium to propodus with 5, 9, 5 and 5 acute spines respectively, those of propodus being more robust than remainder; anterodistal margin of merus and carpus with 4 and 6 spines respectively.

Pleopod 1 exopod with about 37 PMS, and

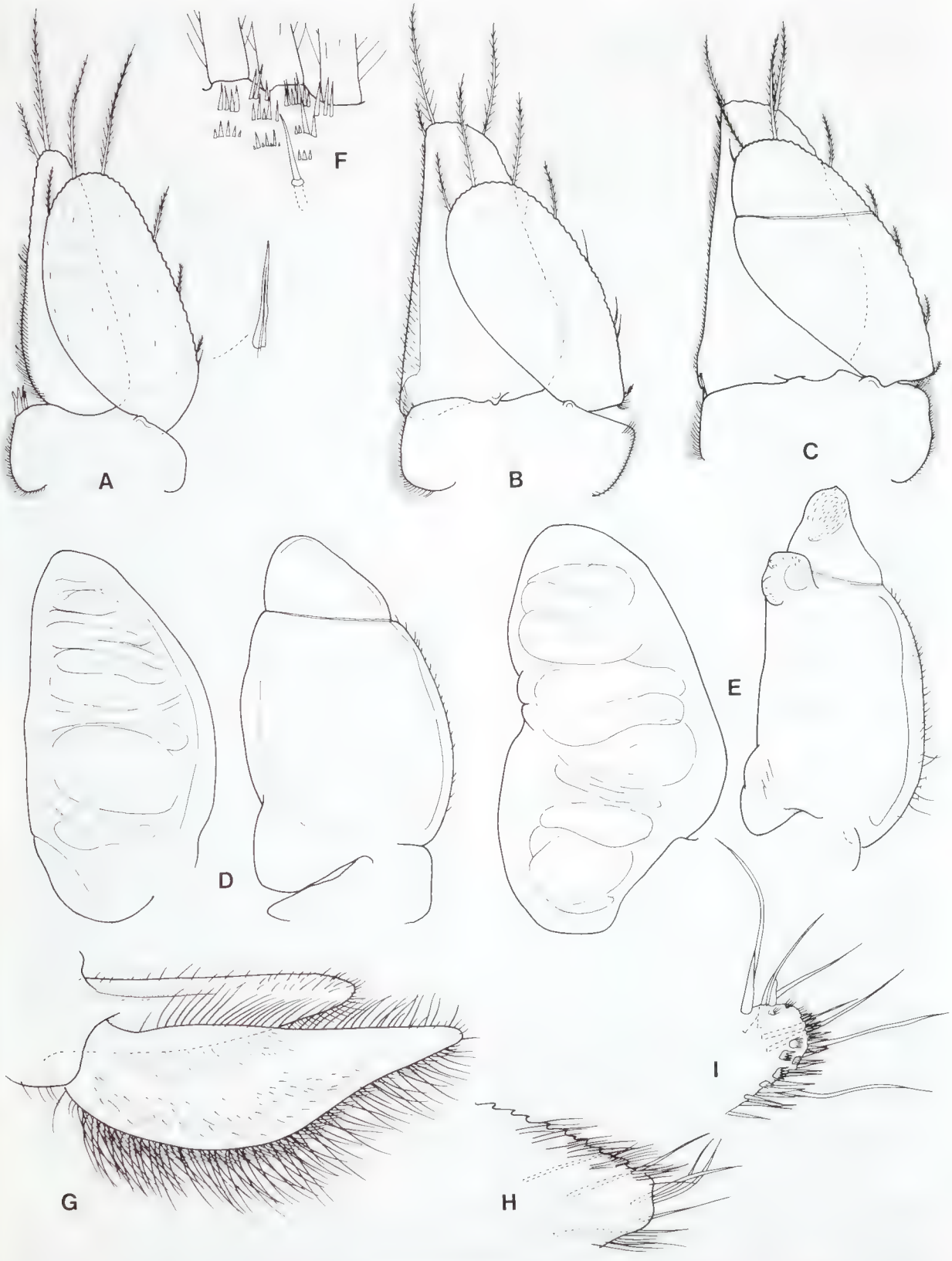


Figure 14. *Xynosphaera colemani* sp. nov., female paratype. A–E, pleopods 1–5, respectively; F, distal margin of pleopod 1 exopod showing scales; G, uropod; H, uropod endopod, apex; I, uropod exopod, apex.

notch, and the short uropod rami, with a reduced exopod. Although the dorsal ornamentation and prominence of the pleotelsonic bosses also identify the species, such ornamentation has in some cases been demonstrated to be unreliable as a defining generic character (Harrison and Holdich, 1982; Bruce, 1994b — *Paracassidina*). The shape of the cephalon is here not regarded as ornamentation, comparable to the nodules and bosses shown by the genera cited above, and the presence of a second species (Masthead I.) indicates that this should be regarded as a defining character for the taxon.

The position of *Bregmotypta* in relation to other genera is not clear, although penial (elongate and distally narrow) and pleopod morphology (pleopod 1 medial margin with groove) suggest the genus belongs to the group of loosely similar genera that includes *Waiteolana* Baker, 1926, *Ceratocephalus* Woodward, 1877 and *Kranosphaera* Bruce, 1992.

Baker (1926: 279 (caption), plate 47, figs. 10, 11) recorded a similar unnamed dry specimen (Sphaeromatidae) from Masthead I., Capricorn Group, southern Great Barrier Reef. I have not been able to locate this specimen, which is now presumed lost but if, as seems probable, this specimen belongs to this genus, its range extends to the subtropical coast of eastern Australia.

### ***Bregmotypta pavicula*** sp. nov.

Figures 15–17

*Material examined.* Holotype. NSW, Jibbon Head (34°05′S, 151°10′E) Sep 1976, 23 m, algae on reef, J.E. Watson, NMV J36943 (♂ 8.2 mm).

Paratype. Same data as holotype, NMV J26421 (♂ 7.8 mm, dissected, 3 slides).

*Description of male.* Body strongly vaulted, about twice (2.1) as long as greatest width; cephalon 25% of total BL; surface of cephalon proximally coarsely pitted, anteriorly coarsely and irregularly ridged. Posterior margin of pereonite 1 with 4 prominent nodules, pereonites 2–7 each with 6, each nodule with apical pit containing setae; laterally pereonites 2–7 with prominent subrectangular lobe, each with apical pit, and large coxal boss. Pleon posterior margin with raised rim, with 2 prominent submesial nodules, each with an apical pit. Pleotelson with 2 bilaterally compressed bosses, concealing posterior margin of pleotelson; pleotelson with 3 obscure nodules dorsal to ill-defined wide notch.

Antennule peduncle article 1 large robust, article 2 short, about 0.4 (0.38) length of article 1; article 3 slender, about 4 times as long as wide, longer than article 2 (1.4); flagellum of 12 articles. Antenna peduncle article 3 shortest; flagellum with 12 articles. Mandible palp articles 2 and 3 with 9 and 18 biserrate setae respectively. Maxilla lateral and middle lobes with 9 and 10 finely serrate setae respectively; mesial lobe with abundant plumose, serrate and simple spines. Maxilliped palp with 18–20 setae each on articles 2–5; endite with blunt biplumose and sinuate acute spines on distal margin.

Pereopod 1 posterior margin of merus, carpus and propodus with 5, 3 and 4 spines respectively; dactylus posterior margin with proximal scales; accessory unguis blunt; anterodistal margin of ischium with 3 acute spines; anterodistal angle of merus with 2 acute spines. Pereopod 2 ischium with 2 acute spines on anterior margin; posterior margins of merus and carpus with dense setule fringe, each with 3 stout acute spines; propodus posterior margin with 4 spines. Pereopod 7 more slender than 2–6, with additional and longer spines on posterior margin of merus, carpus and propodus and distal margin of carpus.

Penes about 4 times as long as basal width, covered with fine scales.

Pleopod 1 with ventral surface with abundant short setules; endopod with about 26 PMS, exopod with about 40 PMS. Pleopod 2 endopod and exopod with about 24 and 44 PMS respectively; proximolateral margin of endopod with small lobe; appendix masculina slightly longer than endopod. Pleopod 3 endopod and exopod with about 21 and 45 PMS respectively. Pleopods 4 and 5 exopods with folds very large and fleshy. Uropod endopod with distal margin subtruncate, lateral margin indenting distal to exopod; exopod short, subcylindrical, about one third (0.34) length of endopod.

*Female.* Not known.

*Distribution.* Known only from the type locality.

Figure 15. *Bregmotypta pavicula* sp. nov. A–E holotype, remainder paratype. A, dorsal view; B, lateral view; C, frons; D, pleon, ventral view; E, posterior margin of pleon in posterior view; F, antennule; G, antenna; H, left mandible; I, left mandible, incisor and lacinia mobilis; J, right mandible, distal part; K, mandible palp; L, maxillule; M, maxillule, lateral lobe apex; N, maxillule, medial lobe spines. Scale 2.0 mm.

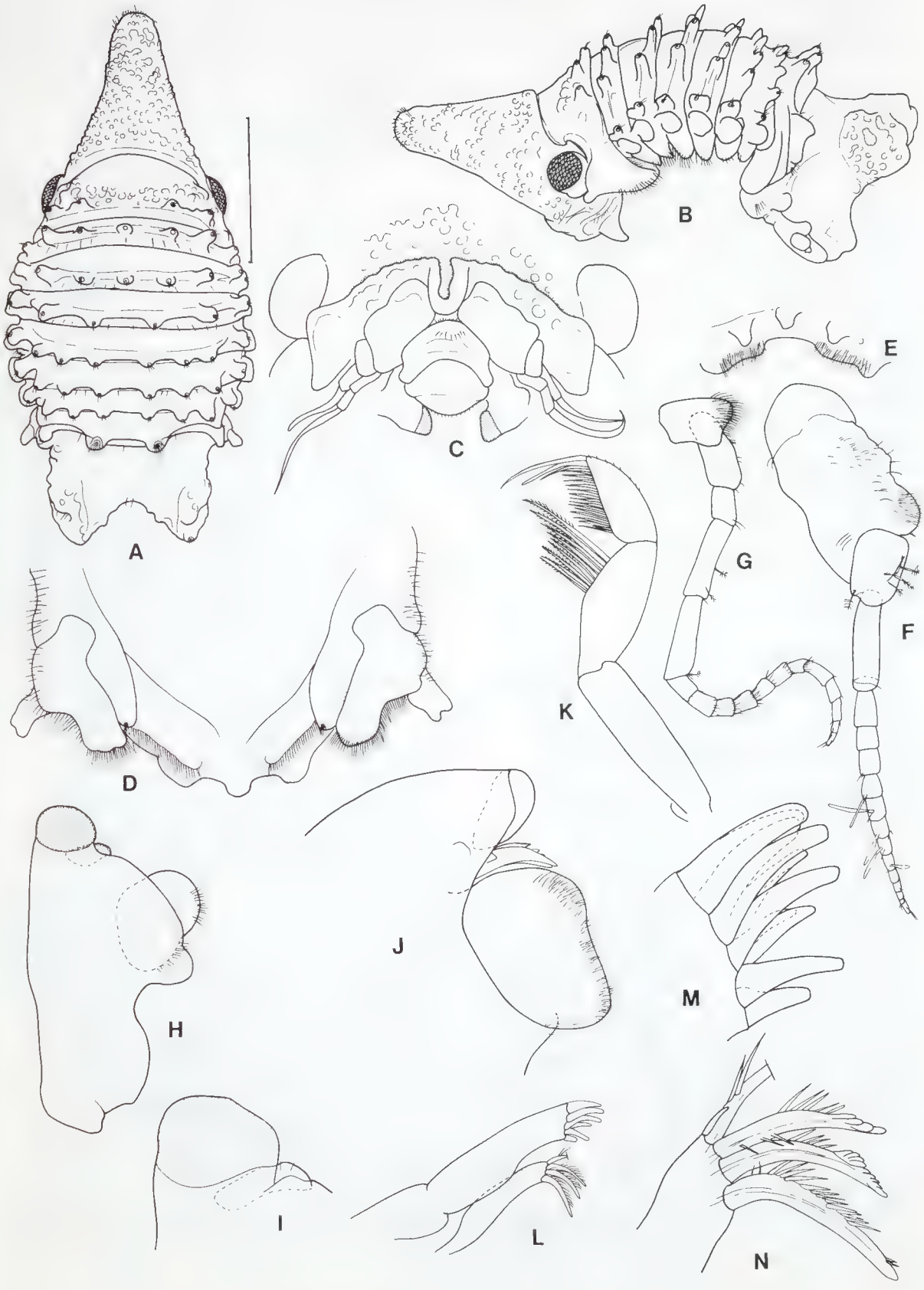
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Figure 16. *Bregmotypta pavicula* sp. nov., paratype. A, maxilliped; B, maxilla, b, spine from maxilla lateral lobe; C, maxilla, medial lobe margin; D, pereopod 1; E, pereopod 1 propodus; F, pereopod 2; G, pereopod 2, distal propodal margin; H, pereopod 7, h, spine from anterodistal angle of carpus, hh, spines from posterodistal angle of carpus; I, penes.

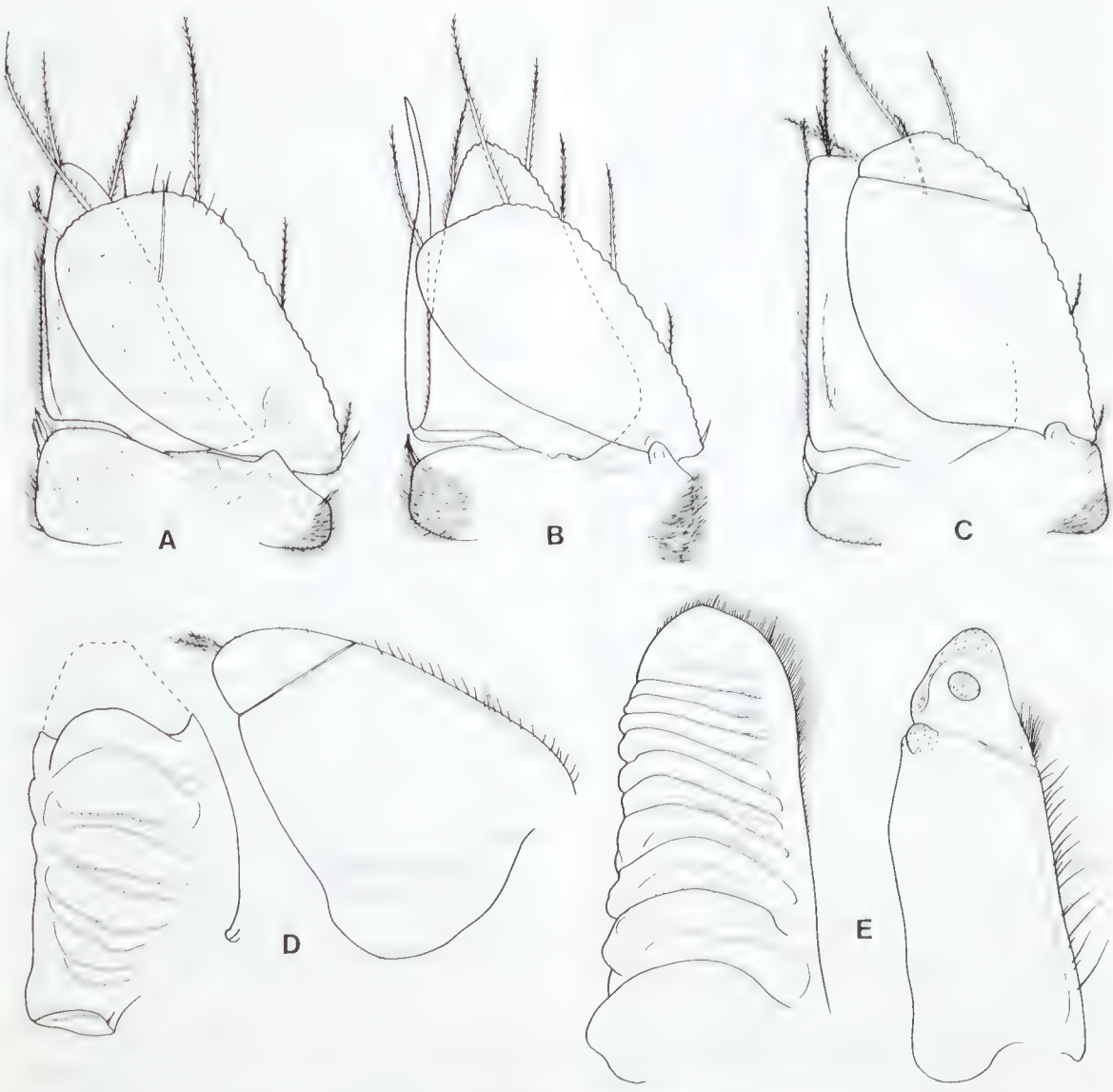


Figure 17. *Bregmotypta pavicula* sp. nov., paratype. A–E, pleopods 1–5, respectively.

*Etymology*. The epithet is a Latin word meaning rammer.

*Remarks*. The species can be identified on the basis of generic characters. The undescribed species recorded from Masthead I. has much larger pleonal processes and smaller telsonic bosses, and lacks prominent nodules on the anterior pereonites.

***Cercosphaera*** gen. nov.

*Type species*. *Cercosphaera wirritin* sp.nov., here designated.

*Diagnosis of male*. Body rugose, nodular, strongly vaulted. Cephalon with ventral rostral process; eyes round, facets distinct. Pereonites 1 and 3, 4 or 5 usually with pair of sublateral bilaterally flattened flanges; coxae on pereonites 2–7 without distinct sutures, overlapping anterior to posterior; pereonite 7 slightly narrower than 6. Pleon composed of 4 segments, segment 1 entire, 2 sutures extending to lateral margin, dorsally with 2 prominent flattened submesial keels. Pleonal sternite absent. Pleotelson prominently bidomed, with posteriorly directed median process on posterior margin; distinct median ventral notch present.

Epistome anteriorly triangular, not extending between antennule bases. Antennule peduncle article 1 massive, calcified, with anteriorly directed process; article 2 short calcified; article 3 slender. Antenna slender; peduncle with article 3 shortest, 4 and 5 longest. Mandible incisor unicusped; molar surface finely granular or smooth, mesial margin with (*C. wirritin* sp. nov.) or without scales (other species); lacinia mobilis present on left mandible; spine row present on right mandible only (type species) or on both mandibles (other species). Maxillule lateral lobe with 11–12 spines on gnathal surface, some of which are feebly serrate, lateral lobe with 4 long spines, robustly serrate. Maxilla with all lobes spinose, many of which are distinctly serrate. Maxilliped palp articles 2–4 mesial margins produced; endite distal margin with peg-like and slender plumose spines.

Pereopods ambulatory, all robust, with prominent setulose fringe; accessory unguis of dactylus simple; pereopod 1 with stout acute serrate spines on posterior margin of merus carpus and propodus.

Penes elongate, folding into groove on mesial margin of pleopod 1 endopod; basally adjacent, not fused.

Pleopods 1–3 both rami with PMS; pleopod 4 exopod with 1–3 apical short PMS. Pleopod 2 appendix masculina attached basally. Pleopod 1 endopod triangular, exopod oblique, subtruncate. Pleopods 3–5 exopod with entire transverse suture. Pleopods 4 and 5 exopods with SMS on lateral proximal margin; pleopod 4 exopod with distomesial margin indented; pleopod 5 with distal margin scaled, 1–2 prominent to scaled lobes on distal part, 1 or 2 scaled lobes present on distomesial angle of proximal part. Uropod exopod nodulose, not extending to posterior of pleon; short, about half as long as endopod, articulating anterolaterally.

*Female*. Similar to male, but antennule peduncle without anterior process; mouthparts metamorphosed; oostegites arising from coxae of pereopods 1–3, possibly 4 (pereopods are very deep set, the single ovigerous specimen is brittle, and mesial margin of the coxa 4 could not be seen clearly) overlapping at midline.

*Distribution*. The genus appears to be restricted to southern and south-western Australian coasts from Dongara, W.A. to Victoria. Given the scarcity of mature specimens, it is probable that habitat of adults is yet to be located.

*Etymology*. The Greek word *kerkos* (tail) in combination with the ending *-sphaera* (feminine).

*Remarks*. The genus is easily separated from all other Sphaeromatinae by the presence of a posteriorly directed telsonic process arising from the posterior point of the pleotelson. The presence of short uropodal rami with the endopod larger than the exopod immediately separates it from those species of the *Cilicaea-Cilicaeopsis* group with a prominent median point in or above the pleotelsonic notch. *Kranosphaera* Bruce, 1992 is similar but the apex of the pleotelson is only weakly produced, and the unique morphology of pereopods 5 and 6 and lack of a uropodal exopod readily separates that genus.

Only the type species is represented by both sexes and immature stages. The adults, immature and manca stages all have similar ornamentation and morphology, except that very small mancas are not as nodular. The species are therefore recognizable by body ornamentation at all stages of development, although it is not known if all species are sexually dimorphic in the ornamentation of the antennule.

Two undescribed species are represented by mancas only. One, from Bass Strait (Fig. 23) at 52 m is similar to *Cercosphaera wirritin* and the other, from off Flinders I., S.A. (NMV J36942), is similar to *Cercosphaera dilkera* sp. nov., but has large keels on pereonite 1.

**Key to species of *Cercosphaera***

1. Pleon with prominent submedian dorsal flanges: body ornamentation of smoothly edged nodules: pleotelsonic process short ..... 2

— Pleon with inconspicuous flanges; body ornamentation of granular nodules; pleotelsonic process long ..... *C. wirritin*

2. Pleonal flanges anteriorly smooth; nodules weak on pereonites 2, 3, 6 and 7; pleotelsonic process distally truncate ..... *C. dilkera*

— Pleonal flanges dorsally irregularly trilobed; nodules weak on pereonites 3, 6 and 7; pleotelsonic process bilaterally narrowed ..... *C. coloura*

***Cercosphaera wirritin*** sp. nov.

Figures 18–22

*Material examined.* Holotype. WA, Seven Mile Beach, north of Dongara (29°12.00′S, 114°53.00′E) 24 Apr 1986, 1 m, epiphytes on *Amphibolis*, NMV J36938 (♀ non-ovig. 5.0 mm).

Paratypes. WA, 1 km west of Red Bluff, Kalbarri (27°42′S, 114°09′E) 9 Jan 1984, 18 m, bryozoa among *Ecklonia*, J.K. Lowry, AM P41121 (♂ 4.5 mm, broken, 2.9 mm). WA, west end of Michaelmas I. (35°02.80′S, 118°01.40′E) 17 Apr 1986, 15 m, G.C.B. Poore and H.M. Lew Ton, NMV J26167 (♀ non-ovig. 6.0 mm). Vic, Laurence Rocks, Portland (38°24.0′S, 141°40.1′E) 30 Apr 1988, 23 m, R.T. Springthorpe and P.B. Berents, AM P41367 (♀ ovig. 5.1 mm).

*Description of male.* Body with coarse tubercles over dorsal surface, cuticular surfaces between tubercles appearing glassy; about 1.7 times as long as wide, widest at pereonite 1; pleotelsonic process about 13% BL; cephalon with anteriorly positioned submedian pair of tubercles more prominent than remaining tubercles; pereonite 1 with lateral margins laterally extended, with prominent sublateral flattened tubercles; pereonite 5 with sublateral prominent tubercles; pereonites 6 and 7 with tubercles weak. Pleon and pleotelson each with pair of prominent elongate submedian tubercles; pleotelsonic process distally blunt, provided with several acute tubercles. Coxae overlapping anterior to posterior, coxal sutures not visible.

Antennule peduncle article 1, nearly half total length of antennule, anterodistal margin produced forming curved horn-like process; article 2 about 0.3 length of article 1; article 1 anterior process about 0.3 length of article; flagellum of 10 articles, each with aesthetascs. Antenna as for genus.

Epistome anterior margin forming blunt point; each anterolateral angle with nodule. Mandible lacinia mobilis simple, blunt; spine row of right mandible with 5 spines, absent on left; mandible palp articles 2 and 3 with 7 and 15 biserrate setae respectively. Maxillule lateral lobe with 12 simple spines; mesial lobe with 4 elongate sparsely plumose spines as well as 2 short simple spines. Maxilla with 5 and 6 setae on lateral and middle lobes respectively, lateral lobe appearing fused to middle lobe; mesial lobe with simple, biserrate and plumose spines. Maxilliped palp articles 2–5 each with about 18–20 setae; endite with 4 feebly sinuate plumose and 3 peg-like plumose spines on distal margin; distomesial angle with single simple spine and dorsally a large serrate spine; endite dorsal surface with dense elongate serrate scale setae (Fig. 19 F).

Pereopod 1 stout, merus with anterodistal margin somewhat produced; anterodistal angles of ischium and merus each with single acute spine; posterior margin of merus and carpus with setulose fringe on distal part; posterior margin of merus, carpus and propodus respectively with 3, 2 and 3 stout apically bifid serrate spines; posterior margin of dactylus with flat cuticular scales. Pereopods 2–7 more elongate than pereopod 1, spines generally more slender and acute; pereopod 2 with 2, 1 and 2 spines respectively on posterior margin of merus, carpus and propodus; anterodistal angles without spines. Pereopod 6 similar, but with acute single spine present on anterior margin of ischium and anterodistal angles of merus and carpus; posterior margin of merus, carpus and propodus with 2, 3 and 3 spines respectively. Pereopod 7 slender, ischium more elongate than 6, almost devoid of setules; spination similar to that of pereopod 6.

Penes slender, about 11 times as long as basal width.

Pleopod 1 endopod and exopod with about 14 and 29 PMS respectively; peduncle distolateral angle with acute spine; proximolateral angle of exopod without acute spine. Pleopod 2 endopod and exopod with about 15 and 30 PMS respectively; appendix masculina straight, extending a little beyond distal margin of endopod, about

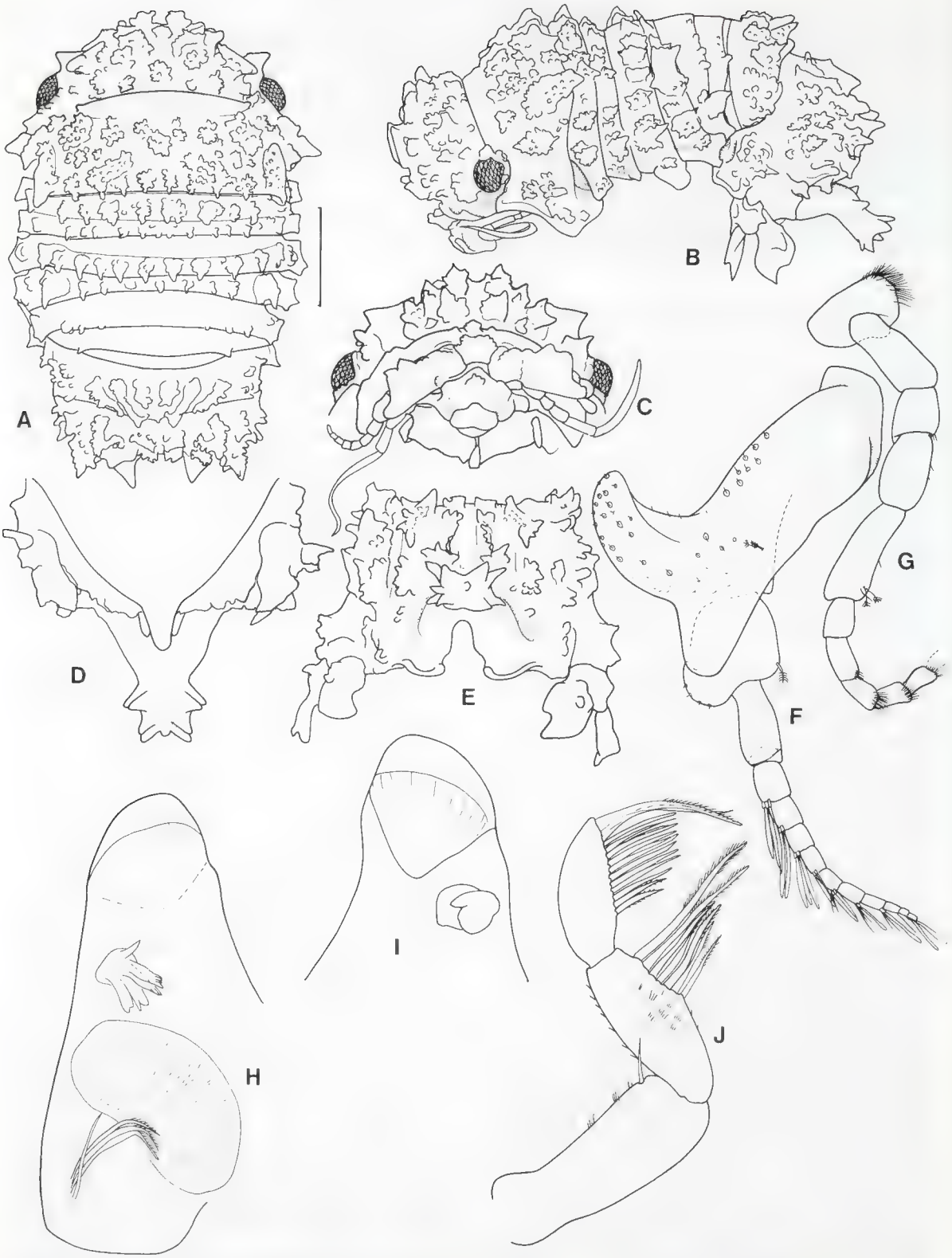


Figure 18. *Cercosphaera wirritin* sp. nov. A–E holotype, remainder ♂ paratype 4.5 mm, AM P41121. A, dorsal view; B, lateral view; C, frons; D, pleotelson, ventral view; E, pleotelson, posterior view; F, antennule; G, antenna; H, right mandible; I, left mandible; J, mandible palp. Scale 1.0 mm.

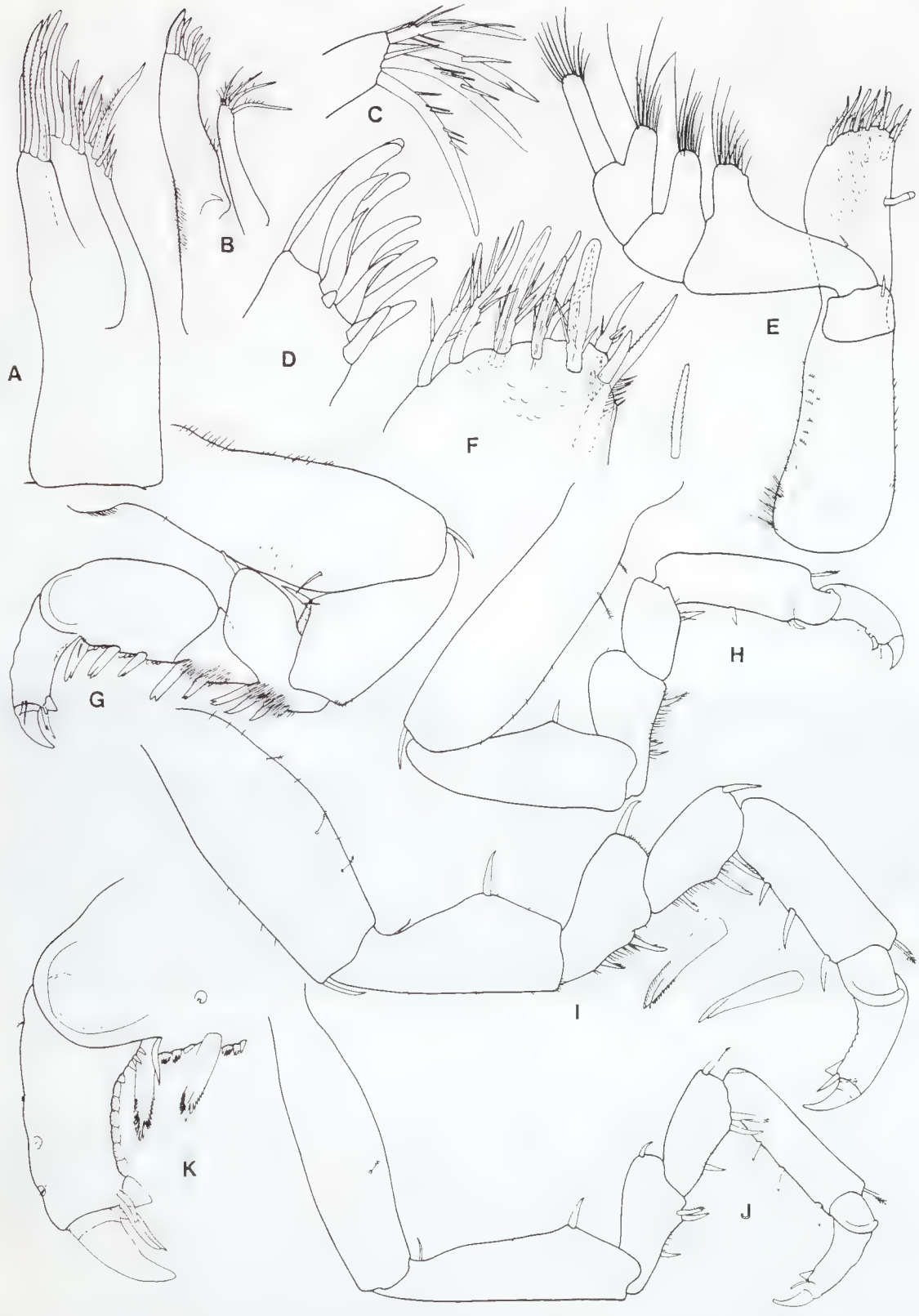


Figure 19. *Cercosphaera wirritin* sp. nov. All figs of ♂ paratype, AM P41121. A, maxilla; B, maxillule; C, maxillule, endopod apex; D, maxillule, exopod apex; E, maxilliped; F, maxilliped endite, distal margin cuticle f, setule from endite distal margin; G–J, percopods 1, 2, 6, 7, respectively; K, pereopod 1, dactylus.

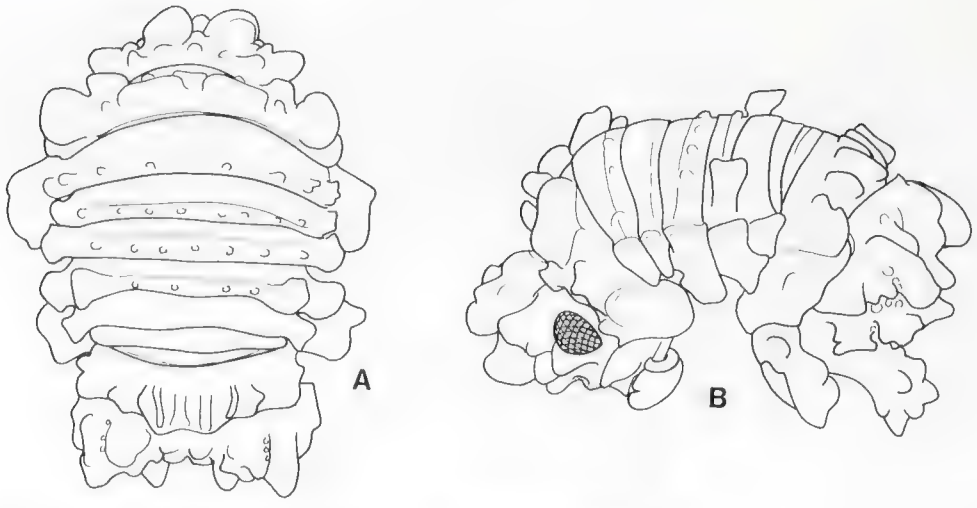


Figure 23. *Cercosphaera* sp., NMV J36941. A, dorsal view; B, lateral view.

*Distribution.* Mid-western coast of Western Australia south and eastwards to Victoria.

*Etymology.* An Aboriginal word meaning rough (noun in apposition).

*Remarks.* The jagged and rough surface of the dorsal tubercles and the glassy appearance of the cuticular surfaces immediately identifies this species, as does the elongate and spiked telsonic process. Compared to other species of the genus the pleonal flanges are small.

The asymmetry of the spine row is extreme compared to the other species of the genus and applies equally to males and non-ovigerous females.

### ***Cercosphaeroma dilkera*** sp. nov.

Figures 24–26

*Material examined.* Holotype. WA, Seven Mile Beach, north of Dongara (29°12.00′S, 114°53.00′E) 22 Apr 1986, 0.5 m, sand patch in *Halophila*, air lift, G.C.B. Poore and H.M. Lew Ton, NMV J26178 (♂ imm, 4.2 mm, 7 slides).

Paratypes. WA, same data as holotype, NMV J37344 (manca 1.5 mm); WA, same data as holotype, except 1.0 m, mixed algae beneath overhang on reef, NMV J26153 (manca 3.0 mm, 1 slide). SA, northeast side of Topgallant I., Investigator Group (33°43.00′S, 134°36.60′E) 21 Apr 1986, 20.0 m, on *Cystophora* spp. and *Plocamium*, G.K. Brandon and G.C.B. Poore, NMV J26201 (manca 2.8 mm). WA, 15 km south of Port Fain (38°32.0′S, 142°28.6′E) 20 Nov 1981, 52 m, medium sand, R. Wilson, ZMUC CRU166 (manca 2.2 mm).

*Description of male.* Body about twice as long as wide, widest at pereonite 1; dorsal surface covered with well spaced rounded nodules; particular prominent, forming "shoulders" at lateral margins of pereonites 2–6; paired prominent submedian nodules present on pereonites 1 and 4; nodules dorsally weak on pereonites 2, 3 and 6, 7. Pleon with very prominent pair of submedian flanges which have smoothly curving anterior margin. Pleotelson process short, about 7% BL, apex medially indented, distinctly truncate in lateral view.

Epistome anteriorly narrowed and blunt. Antennule peduncle article 1 with anterodistal margin weakly produced. Mouthparts similar to type species except mandible: left mandible with prominent lacinia mobilis and spine row of 5 serrate spines, molar with fringe of acute scales and finely punctate surface; right mandible similar to left but lacking lacinia mobilis; spine row with a clubbed spine.

Pereopods similar to type species but setulose fringe entirely absent, and all spines acute.

Pleopods similar to type species but pleopod 1 exopod with acute spine at proximolateral angle and spine on lateral margin of peduncle. Uropod rami flat, distally both rami subtruncate, exopod folds under endopod, about 0.6 length of endopod.

*Size.* Present material consisted of one immature male (4.2 mm) and several mancas (1.5–3.0 mm).

*Distribution.* Mid-western coasts of Western Australia, eastwards to South Australia and Victoria.

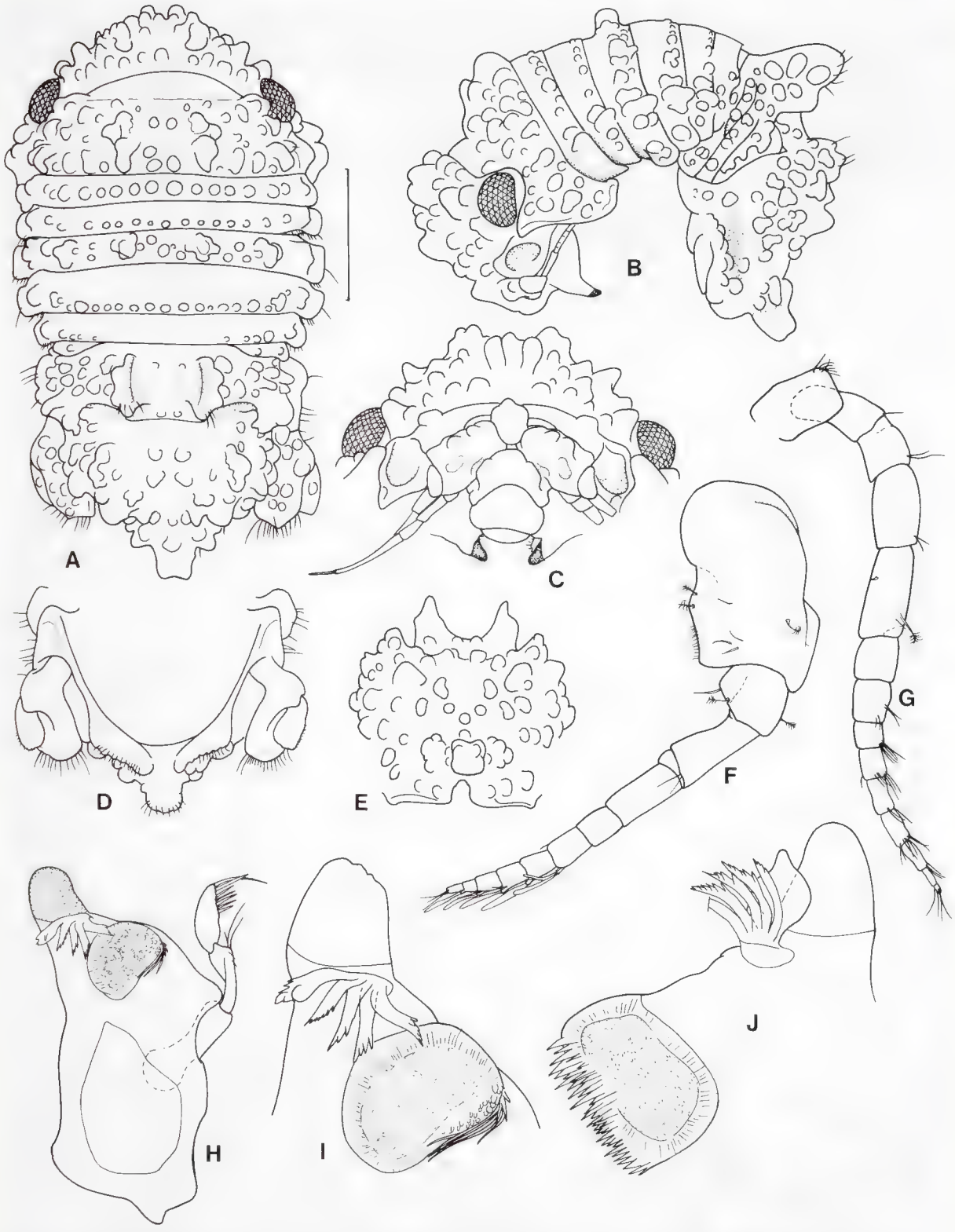


Figure 24. *Cercosphaera dilkera* sp. nov. A–E holotype, remainder 3.0 mm paratype, NMV J26153. A, dorsal view; B, lateral view; C, frons; D, pleon, ventral view; E, pleon, posterior view; F, antennule; G, antenna; H, right mandible; I, right mandible, distal part; J, left mandible, distal part. Scale 1.0 mm.

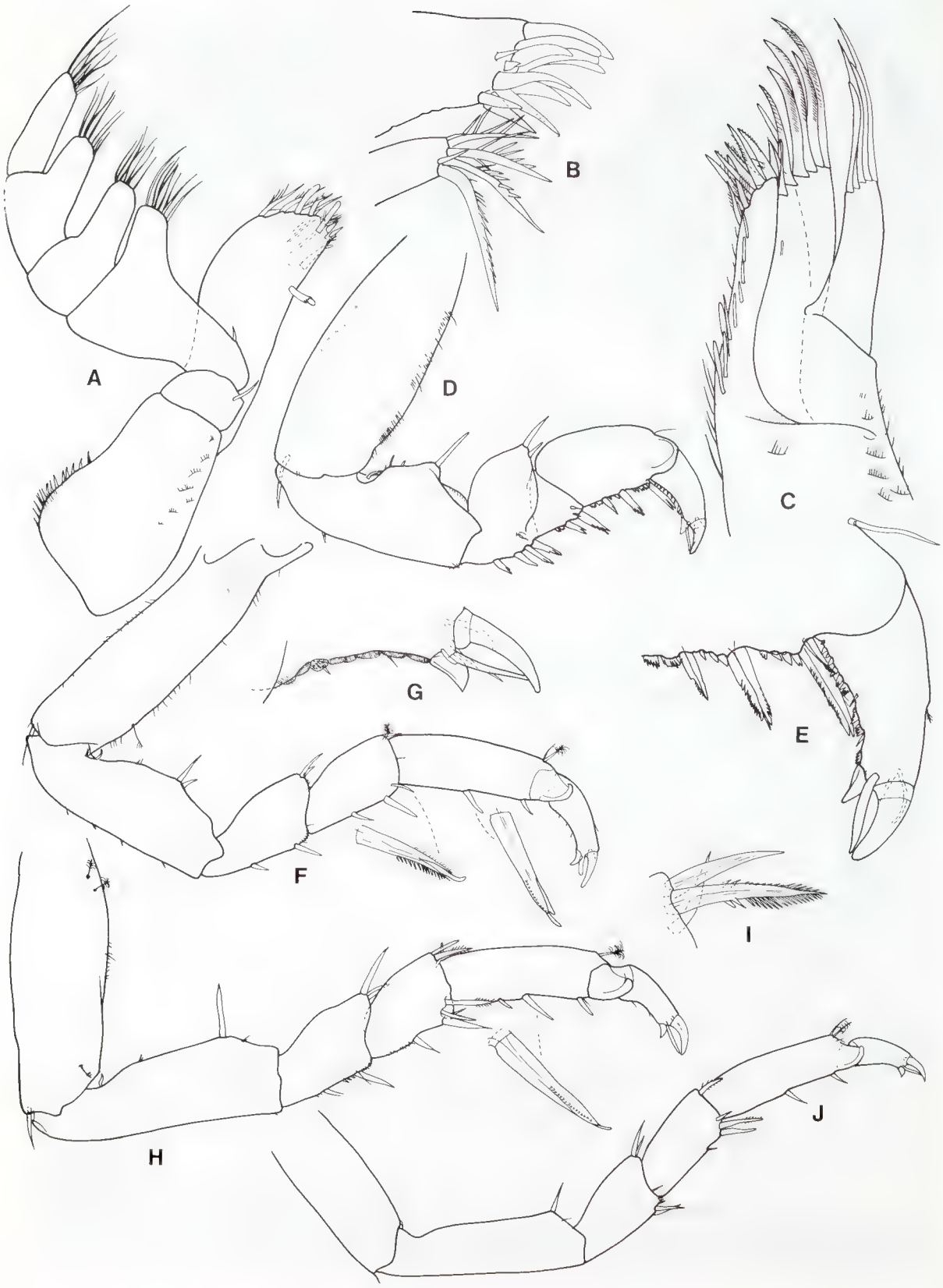
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Figure 25. *Cercosphaera dilkera* sp. nov. A–C paratype, NMV J26153, remainder holotype. A, maxilliped; B, maxillule; C, maxilla; D, pereopod 1; E, pereopod 1, distal propodus and dactylus; F, pereopod 2; G, pereopod 6; H, pereopod 6, spines on anterodistal angle of carpus; I, pereopod 7.

*Etymology. Dilkera* is an Aboriginal word meaning shore (noun in apposition).

*Remarks.* The short truncate pleotelsonic process and large pleonal flanges readily separates mancas and immature specimens. The characters of body ornamentation are persistent through all observed growth stages for the other species of the genus, and adults should equally be recognized by these characters.

**Cercosphaera coloura** sp. nov.

Figures 27–30

*Material examined.* Holotype. SA, northeast side of Topgallant I., Investigator Group (33°43.00′S,

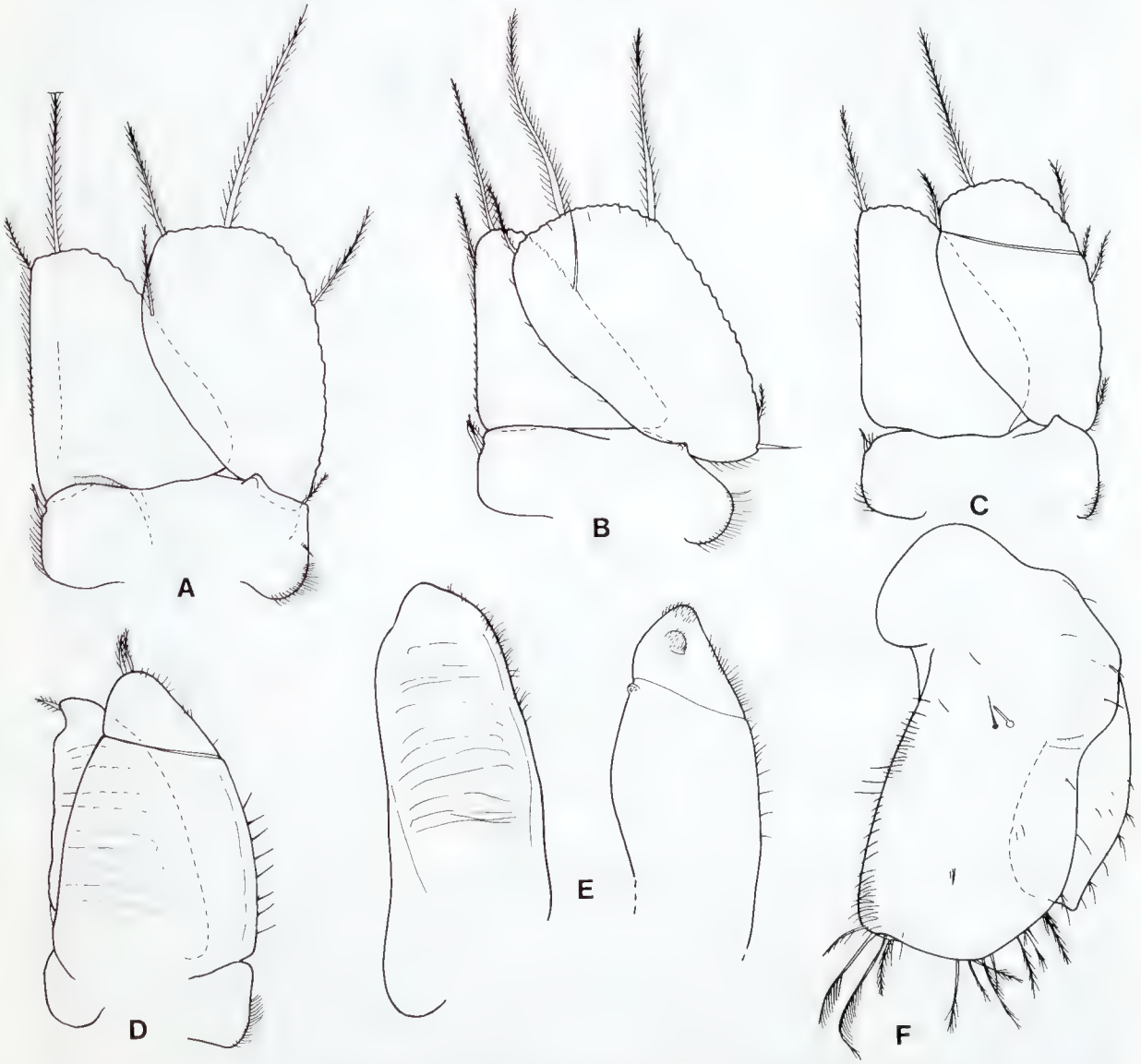


Figure 26. *Cercosphaera dilkera* sp. nov. A–E holotype, remainder paratype, NMV J26153. A–E, pleopods 1–5, respectively; F, uropod.

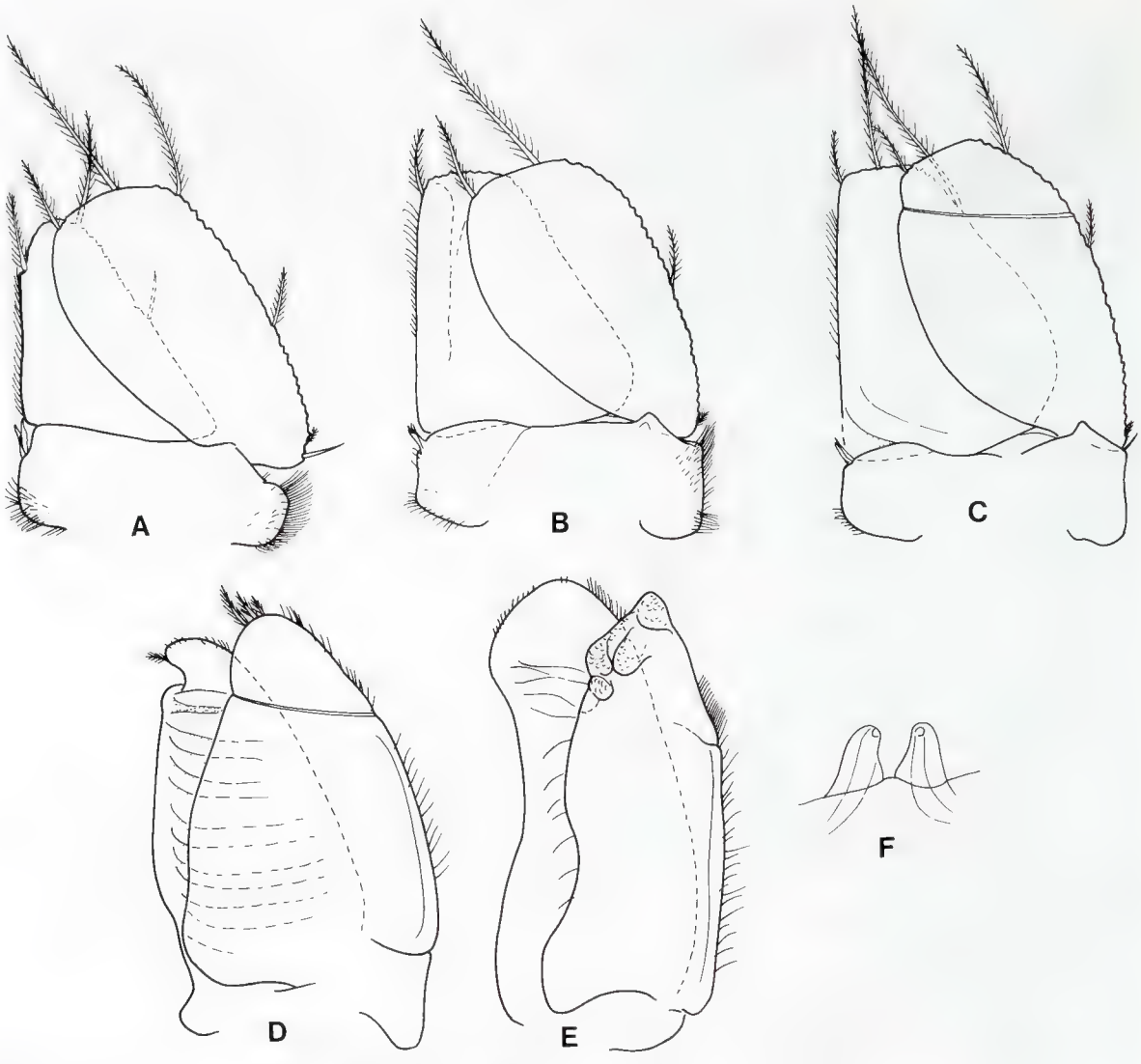


Figure 29. *Cercosphaera coloura* sp. nov. All figs paratype, SAM C5544. A–E, pleopods 1–5, respectively; F, penes.

nodules dorsally weak on pereonite 7. Pleon with prominent pair of submedian flanges, which have an irregular dorsal surface. Pleotelsonic process short, about 6% BL, distally forming a point in dorsal view, truncate in lateral view.

Epistome, antennule and antenna similar to *C. dilkera*. Mouthparts similar to *C. dilkera* except maxillule mesial lobe spines with few spinules.

Pereopods similar to *C. dilkera*, but generally with more and more slender spines.

Paired penes present on sternite 1.

Pleopods similar to *C. dilkera*, but pleopod 5 exopod with weak transverse suture and more prominently scaled distal margin. Uropod rami nodular, endopod narrowing distally to oblique posterior margin; endopod distal margin concave, dorsolateral margin with prominent tubercle; exopod 0.66 length of endopod.

*Female.* Adult females not observed.

*Size.* 6.8–7.8 mm.

*Distribution.* Investigator Archipelago and Kangaroo I., South Australia; Apollo Bay, Victoria.

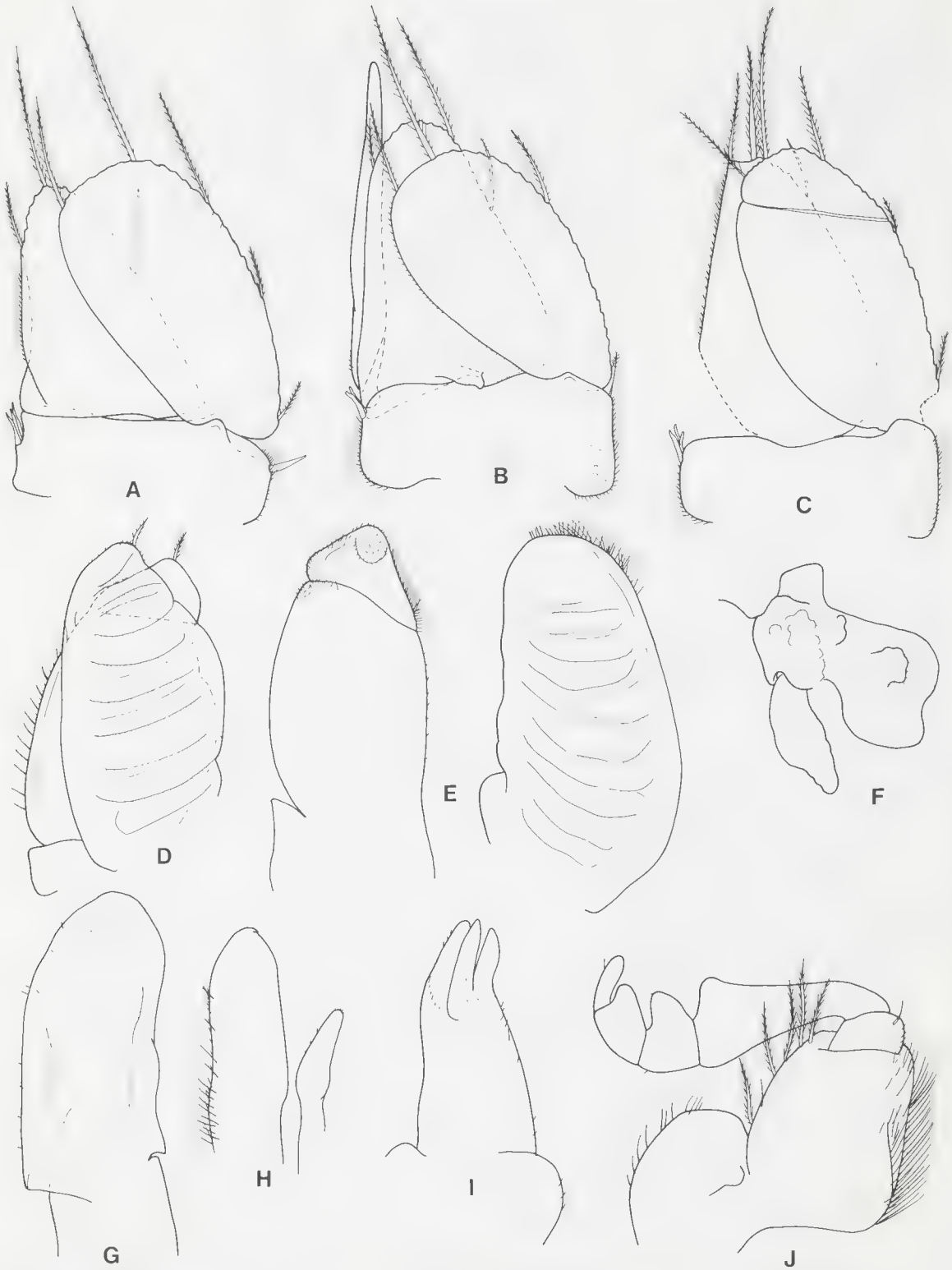


Figure 20. *Cercosphaera wirritin* sp. nov. A–F ♂ paratype, AM P44121, G–J ovig. ♀ paratype, AM P41367. A–E, pleopods 1–5, respectively; F, uropod; G, mandible; H, maxillule; I, maxilla; J, maxilliped.

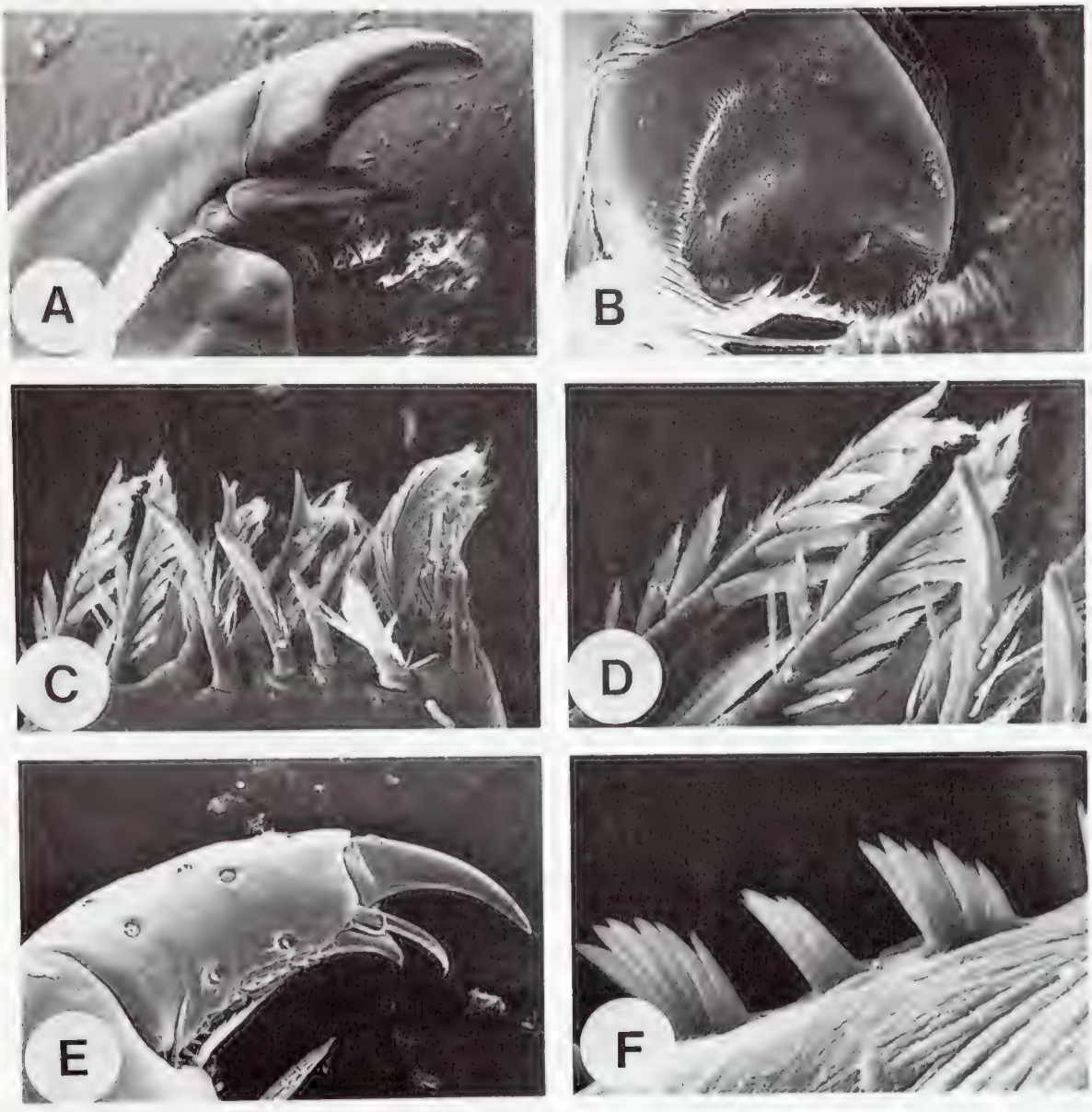


Figure 30. *Cercosphaera coloura* sp. nov. SEMs. A, left mandible (180 ×); B, mandibular molar process (350 ×); C, maxilliped endite, distal margin (550 ×); D, maxilliped endite, distal bipectinate seta (1000 ×); E, pereopod 1, propodus (270 ×); F, pereopod 1, cuticular scales on posterior margin of merus (3000 ×).

*Etymology.* The Greek word *kolouros* meaning bobtailed.

*Remarks.* This, the largest species of the genus, is recognized by the arrangement and distribution of the tubercles, and by the shape of the pleonal flanges and pleotelsonic process. The prominence of the flanges and short pleotelsonic process separate *C. coloura* from *Cercosphaera dilkera*, which being about half the size of *C. coloura*, is otherwise similar. The flanges on *C. coloura* arise abruptly and have an irregularly trilobed distal surface while those of *C. dilkera* are larger and curve smoothly from the anterior with a swept-back appearance. The pleotelsonic process of both species also differ, that of *C. coloura* being bilaterally acute, while that of *C. dilkera* is blunt or subtruncate with a median indentation. The appendages of the two species, which have overlapping ranges, are similar.

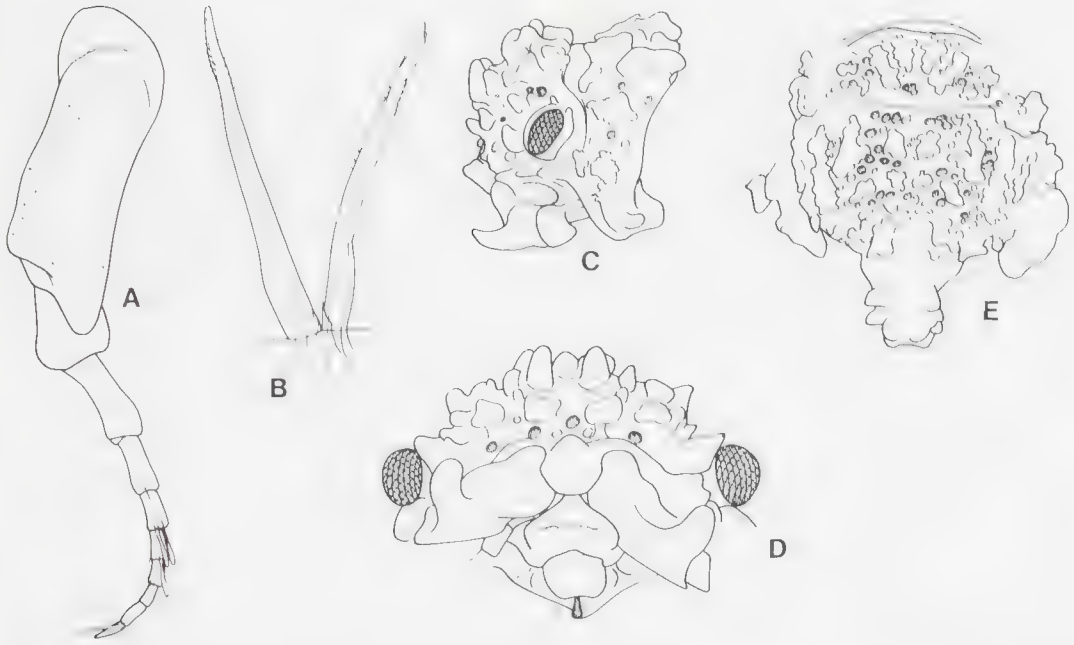


Figure 21. *Cercosphaera wirritin* sp. nov. A ♀, AM P41367, remainder ♂ paratype 4.5 mm, AM P41121. A, antennule; B, penes; C, cephalon, lateral view; D, cephalon, frons; E, pleotelson, dorsal view.

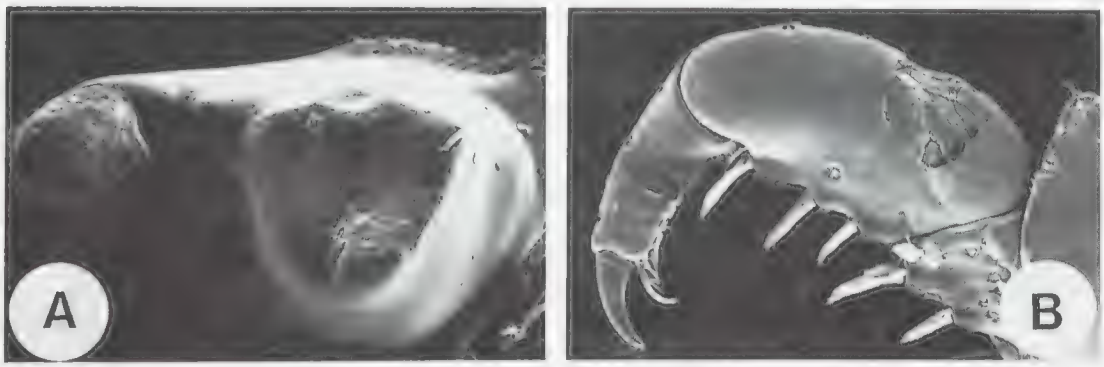


Figure 22. *Cercosphaera wirritin* sp. nov. SEMs. A, right mandible, showing incisor and molar process (190 ×); B, pereopod 1, propodus (200 ×).

1.3 times as long as endopod. Pleopod 3 endopod and exopod with about 10 and 28 PMS respectively. Pleopod 4 both rami each with single short apical PMS. Pleopod 5 with scale patches at distomesial angle of proximal part and a ventral scaled lobe; distal margin all scaled. Uropod endopod nodular, widest posteriorly, rounded with distal indentation and lateral flat lobe; exopod curving, with narrowly rounded apex, set separately to and not overlapping endopod.

*Female.* Similar body ornamentation to the male but lacking the anterior process on antennule peduncle article 1. Mouthparts (Fig. 20) and brood pouch as for the genus.

*Colour.* White, pereopods 4–6 with band of dark brown chromatophores on ischium and propodus of some specimens.

*Size.* A small male, with anterior process, measured 2.9 mm, otherwise adults 4.5–6.0 mm.

**Acknowledgements**

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Memoirs of the Museum of Victoria 54(2): 439–445 (1994)

# A NEW SPECIES OF THE FRESHWATER CRAYFISH GENUS *ENGAEUS* ERICHSON (DECAPODA: PARASTACIDAE) FROM NORTH-WESTERN TASMANIA

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## Abstract

Horwitz, P. 1994. A new species of the freshwater crayfish genus *Engaeus* Erichson (Decapoda: Parastacidae) from north-western Tasmania. *Memoirs of the Museum of Victoria* 54 (2): 439–445.

A new species of freshwater crayfish, *Engaeus yabbimunna*, is described from Burnie in north-western Tasmania. The species can be readily distinguished by using characters established in the most recent revision of the genus *Engaeus*, notably the nature of the chelae, form of rostrum and the antennal flagella. It is proposed that the new species has a restricted geographical range (not unusual for species in this genus), and that it is found in and around the city of Burnie. Its absence from previous extensive collections, its absence from parts of Burnie, and the restricted nature of the distribution, together highlight the need for adequate protection of the species.

## Introduction

The genus *Engaeus* contains 34 species, 12 endemic to Tasmania (Horwitz, 1990). This paper reports on another endemic species from the Burnie region in north-western Tasmania. The following description follows the format and uses the same abbreviations of Horwitz (1990).

### *Engaeus yabbimunna*

Figure 1

*Material examined.* Holotype. Burnie Park, from burrow in seepage area in gully of Shorewell Creek below Oldacre Falls (GR 8015 068 551), P. Horwitz, 9 Dec 1992, Museum of Victoria NMV J34474 (male, OCL 25.7 mm.)

Allotype. Type locality, NMV J34475, berried female, OCL 24.0 mm.

Paratypes. Type locality, Queen Victoria Museum QVM:10:11235, berried female, OCL 23.2 mm; burrow in ferny gully in Reserve Park on Romaine Creek, Burnie (GR 8015 080 513), Tasmanian Museum and Art Gallery G3529, P. Horwitz, 10 Dec 1992, male, OCL 25.0 mm.

Other specimens. Type locality, 1 male, 1 female and 2 juveniles; type locality, Bill Walker, Feb 1992, 1 female, one juvenile; Cooee Creek in Burnie (GR 8015: 056520), from burrow in bank, 10 Dec 1992, P. Horwitz, 1 male; Romaine Creek (as for paratype), 1 male, 1 female.

*Description.* Rostrum length variable but usually extending to junction of penultimate and distal segments of antennular peduncle, broad, anteriorly upturned to produce a bold spine. Rostral carinae conspicuous, tuberculate along length (but occasionally inconspicuously so), otherwise smooth, long, fading out well beyond posterior of rostrum, widely separated and ending abruptly almost at anterior of rostrum, not fusing with rostral rim; intracarinate region depressed and U-shaped (in transverse), deep and asetose (except for small single setae in row along the inner margin of each carina). Suborbital angle variable; postorbital ridges low and blunt. Eyes relatively small but pigmented area not reduced on orbital peduncle; antennal flagella short, not extending beyond posterior edge of carapace; antennal scale moderately long and usually extending to distal segment of antennal peduncle, 0.3 as wide as long and with long tapering sharp conical terminal spine and carinate lateral edge. Antennules biflagellate with inner flagellum 0.5–0.6 as long as outer. Interantennal scale generally triangular but variable on that theme, with median longitudinal ridge or swelling. 3rd maxilliped with raised (tuberculate or spined) mesioventral corner of coxopodite; ischium with broad, largely asetose ventrolateral surface, with carinate lateral edge and laterodistal corner produced to short spine; exopodite either absent or shaft-like and less than 0.2 as long as ischium.

Carapace vaulted; areola 0.3–0.4 as wide as long. Carapace granulate on branchiostegal, mandibular, antennal and orbital regions. Cervical groove deepest at meson, V-shaped.

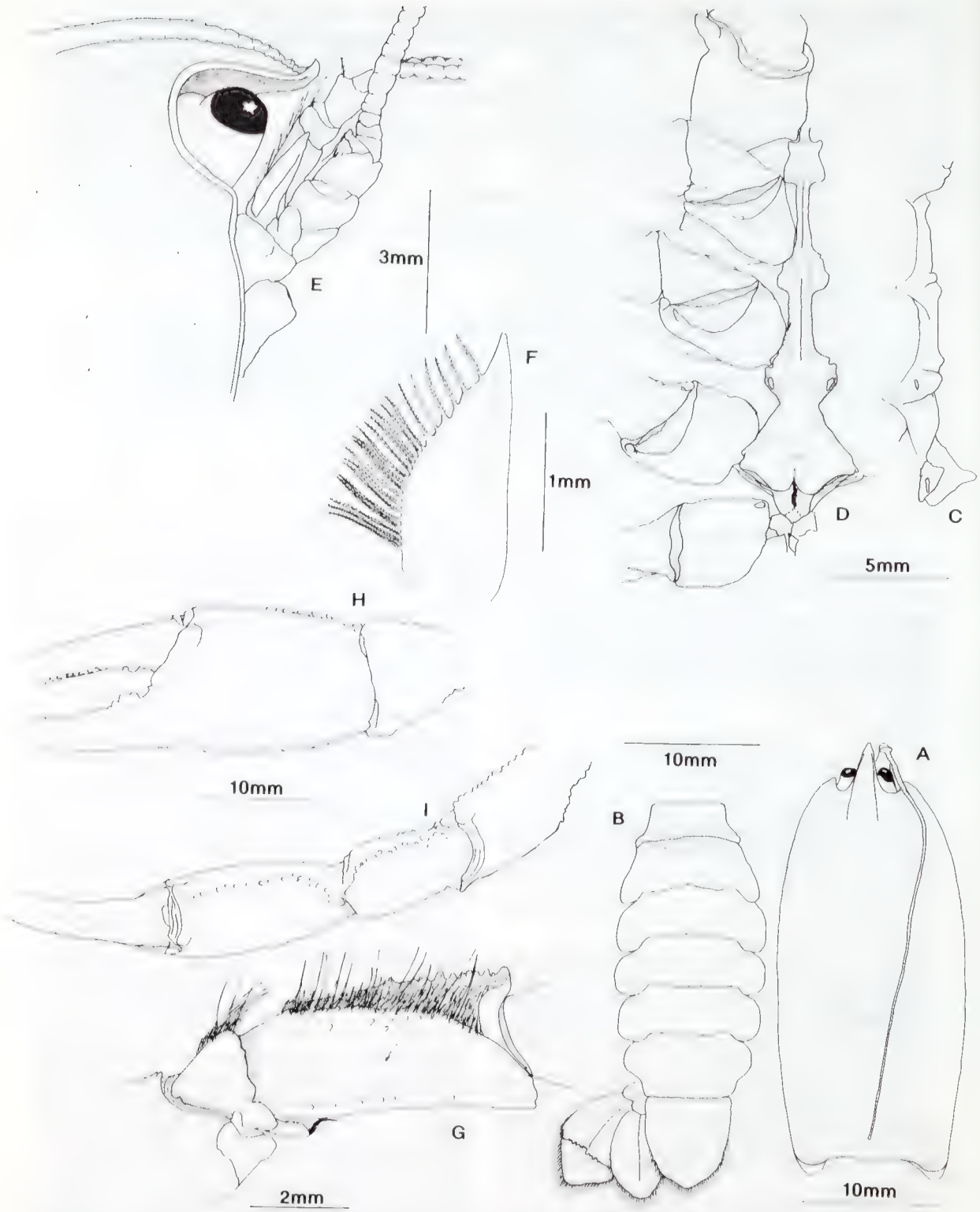


Figure 1. All diagrams are of the holotype. A, dorsal view of carapace; B, dorsal view of abdominal somites and elements of the tail fan (telson and the inner and outer ramus of one uropod); C, lateral profile of sternum (from right side of specimen); D, ventral view of sternum; E, lateral view of anterior cephalon; F, dorsal view of right antennal scale; G, ventral view of third maxilliped (from left side of specimen) showing coxopodite, basipodite, ischium and exopodite; H, lateral view of carpus, propodus and dactyl of left chela; I, dorsal view of carpus, propodus and dactyl of left chela.

TAL 1.08–1.17 × OCL. AP1 reduced in width and with narrow pleura not overlapped by forward extension of pleura of AP2.

Telson broad and well rounded caudally; each caudolateral corner with either a conspicuous spine, a small spine or a notch only; outer ramus of uropod with prominent longitudinal median carina, terminating in median spine on suture; suture straight, with 1–4 extra dorsomesial spines and with 0–4 extra (usually smaller) dorsolateral spines; caudolateral corner with 0, 1 or 2 spines on edge. Inner ramus with or without 1 spine at caudolateral corner, with longitudinal median carina which fades out premarginally.

Chelae isomorphic, largely non-granulate and asetose. Propodal palm with single row of rounded tubercles along dorsal edge, non-granulate and asetose laterally and mesially, and with tuberculate carina along ventral edge. Dactyl dorsally granulate or non-granulate. Carpus smooth dorsally and laterally, without centrodorsal depression and with row or band of small tubercles along dorsomesial edge. Merus with row or band of small tubercles along dorsal edge.

Sternal keel commencing between LP 1st P rising to low peak and then continuing as low but thin ridge, fading at articulations of 2nd P before rising to low ridge, continuing to slight saddle and rising again to fade out at 3rd P articulation level, then recommencing as broad, low ridge and terminating at articulation level of 4th P. LP 1st and 2nd P without pores, otherwise conspicuously raised; LP 3rd P each with pore opening posterolaterally, peaked at articulations and much higher than keel summit; LP 4th P with long slit like pores (beneath posterior rim, opening posterolaterally) and separated by deep Y-shaped valley. Bullar lobes with processes sloping anteromesially, separated by deep, sharp groove and bluntly pointed posteriorly.

Individuals either with male or female gonopores only (no intersexed specimens found). Gill formula usually 21 + ep (posterior pleurobranch reduced to a short fleshy stump).

*Holotype Male*

*Cephalon.* Rostrum moderately long and broad, extending to middle of distal segment of antennular peduncle, 0.11 × OCL, spineless, with straight lateral edges converging to upturned, bluntly pointed tip, whole rostrum curved downwards in lateral profile, bordered entirely by thin rim and dorsolaterally extremely steep and concave between rim and carinae. Rostral carinae conspicuous, straight, converging anteriorly to end very abruptly but neither fusing with themselves nor with the rostral rim, widely separated, tuberculate over at least anterior half, and long (approximately 1.5 × as long as rostral length) fading out posteriorly beyond level of posterior edge of orbit; intracarinate region broadly U-shaped (in transverse), becoming slightly deeper and minutely setose along inner margin of carinae. Suborbital angle obtuse, approximately 110°; postorbital region moderately deeply depressed dorsoposteriorly; postorbital ridges short, bluntly raised; notch in orbital rim absent. Eyes small but pigmented area not reduced on orbital peduncle; eyes extending halfway along rostrum. Antennal flagellum short, extending to posterior edge of carapace, 1.08 × OCL; antennal scale moderately short, extending to just beyond junction of penultimate and distal segments of antennal peduncle, 0.08 × OCL, 0.30 × as wide as long and widest at proximal two-fifths with conical, terminal spine occupying one-fifth of scale length, with distinctly carinate and straight ventrolateral edge to spine, and long plumose setae along mesial edge. Antennules biflagellate with inner flagellum 0.53 × as long as outer and outer 0.28 × OCL. Interantennal scale broad with diverging lateral edges to rounded lateral corners before converging to rounded tip; centroventrally inflated. 3rd maxilliped with mesioventral corner of coxopodite raised and ridge-like, with one large and one smaller apical tubercles; ischium with long bristle setae and short plumose setae along ventromesial surface (becoming sparse mesially and distally), with punctate, granulate and very sparsely setose, broad ventrolateral surface with carinate lateral edge (carinae with minute tubercles along length) and spiniform laterodistal corner; exopodite reduced to a short stump (0.07 × as long as ischium).

*Carapace.* Vaulted, 0.85 × as wide as deep; areola narrow, 0.35 × as wide as long (grooves faint). Branchiostegites (particularly anteroventrally), mandibular, antennal and orbital regions of carapace granulate; areola and dorsal cephalon sparsely, minutely punctate; dorsolateral cephalon glabrous. Cervical groove deep at meson and broadly V-shaped.

*Abdomen.* TAL 1.09 × OCL. AP1 reduced in width, 0.51 × CTW and with unilobed pleura (lobe small and swollen), not distinctly overlapped by forward extension of pleura of AP2. Terga and pleura of AP2–6 minutely punctate and largely asetose.

*Tail Fan.* Telson with tapering lateral sides to caudolateral corners (each produced to small spine) and rounded caudal tip; dorsal surface minutely punctate and setose, with shallow depressions laterally and with longitudinal, central groove caudally; caudal edge with long plumose and short bristle setae. Outer ramus of uropod with short, fine bristle setae along lateral edge, with low, longitudinal median carina terminating on transverse suture in median spine; suture with 3 or 4 extra spines dorsomesially and 4 extra smaller spines dorsolaterally; suture itself moderately straight and deeply impressed along length; caudolateral corner with 2 widely separated spines on one ramus and none on the other; caudal section of ramus with central longitudinal groove fading out before caudal tip, otherwise with indistinct, minute carinae radiating from suture caudally, with short bristle setae and

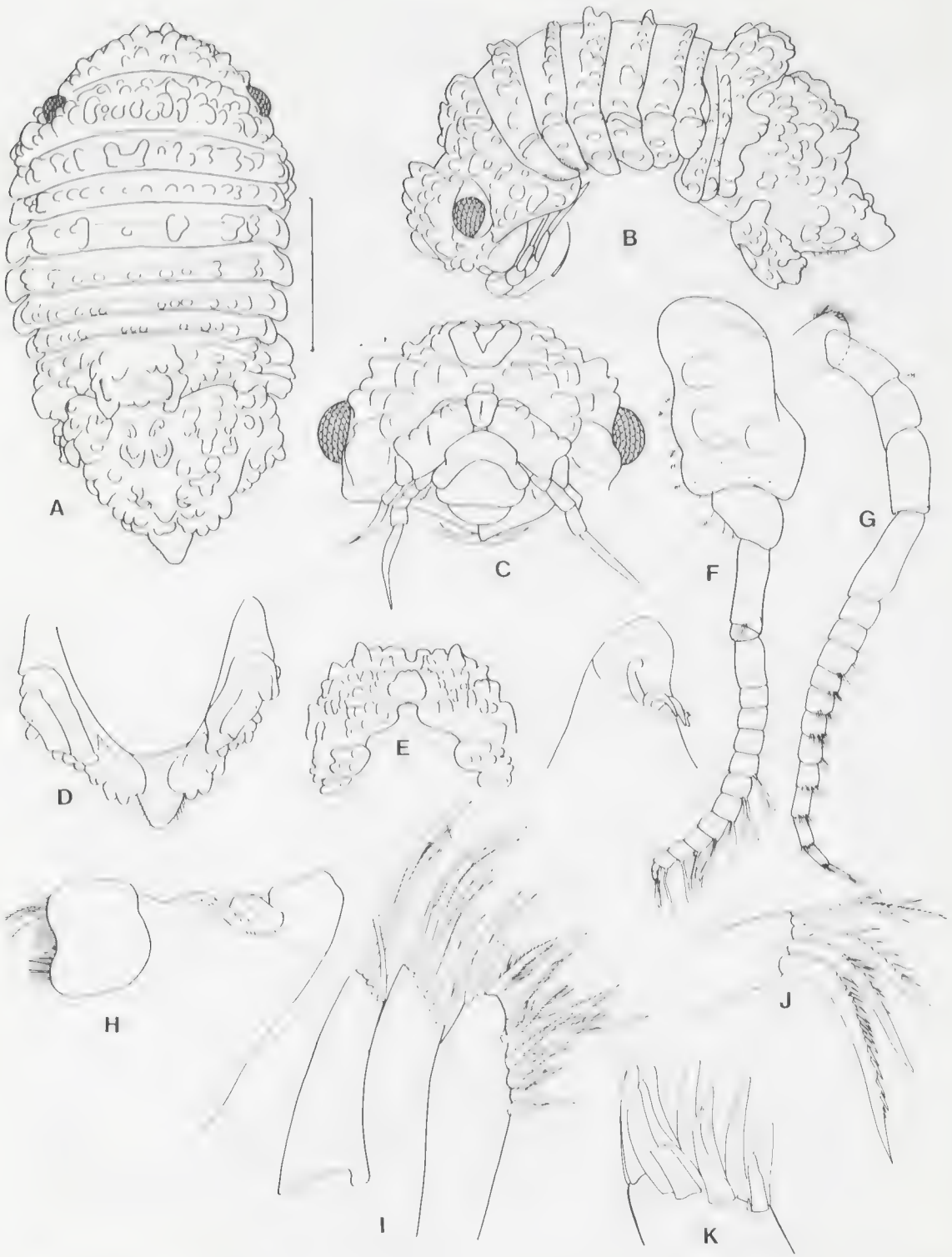


Figure 27. *Cercosphaera colotura* sp. nov. A–E holotype, remainder paratype, SAM C5544. A, dorsal view; B, lateral view; C, frons; D, pleon, ventral view; E, pleon, posterior view; F, antennule; G, antenna; H, left mandible; I, right mandible; J, maxilla; K, maxillule endopod; L, maxillule, exopod. Scale 2.0 mm.

longer plumose setae, along caudal edge; outer ramus constricted at caudolateral and caudomesial corners. Inner ramus of uropod minutely granulate and setose on dorsolateral half, with prominent median carina extending almost entire length of ramus terminating without spine; ramus dorsocaudally minutely striate; caudolateral corner without spine at edge; caudal edge with long plumose and short bristle setae; ramus somewhat leaf-shaped in outline. Inner ramus of uropod extending to beyond telson caudally, outer ramus marginally beyond that. Uropodal peduncle with both lobes rounded and asetose.

*Chelae.* Isomorphic, elongate and largely asetose and non-granulate: DACL/PROPL, 0.59; PROPW/PROPL, 0.43; PROPD/PROPL, 0.25; PROPL/OCL, 0.99. Left chela: propodal palm with only very sparse punctations laterally and mesially; dorsal edge with 15 tubercles in row along entire edge; perpendicular groove indistinct; ventral surface carinate (with row of tubercles along carina proximally). Propodal finger with row of punctations laterally defining the continuation of the carina (from ventral surface of propodal palm), otherwise smooth; cutting edge with 1 large compound tooth in proximal corner followed by 8 small teeth along edge to tip. Dactyl smooth but with 3 longitudinal rows of punctations (dorsal, dorsomesial and dorsolateral) and with one row of sparsely separated small tubercles dorsomesially; cutting edge with 13 teeth decreasing in size over proximal two-thirds of edge, followed by scale setae to tip. Carpus with very shallow centrodorsal groove, with tuberculate ventral projection and sparsely punctate laterally and dorsally, with row of tubercles along lateral edge, row of tubercles along dorsomesial edge (clustered proximally) and extra, small tubercles along ventral area of mesial triangle; otherwise smooth. Merus with glabrous mesial surface; with glabrous lateral surface sparsely granulate dorsally; dorsal surface with prominent dorsal spine amongst a double row of spiniform tubercles along edge; ventral surface granulate centrally, and with tubercles continuous along mesial and lateral rows.

Right chela slightly smaller than left; as for left chela except: 16 tubercles in row along dorsal edge of propodus, 1 small tooth followed by 1 compound tooth and 8 small teeth along cutting edge of propodal finger, and dactyl with 12 teeth along cutting edge.

*Sternum.* 1st P: keel present as low rounded ridge at posterior of LP, rising immediately to small peak then as ridge continuing to 2nd P; LP posteroventrally setose, conspicuously raised but without pores, separated by narrow, moderately deep channel (becoming broader and fading out at posterior level of processes). 2nd P: keel fading out between articulations, then rising to thin crest between LP and beyond, slightly lower than LP at articulations, before decreasing in height to saddle between 2nd and 3rd P; LP posteroventrally setose, distinctly raised, without pores, and separated from keel on either side by narrow, shallow channel. 3rd P: keel rising to low peak before fading out completely at articulation level, then rising to low broad ridge before dropping steeply at articulation level of 4th P; LP 3rd P very high (higher than keel summit) distinctly peaked at articulations, each with pore opening posterolaterally, separated from keel on either side by narrow channel. 4th P: keel as described above; LP peaked at articulations, ridged caudally, with large slit-like pore beneath posterior rim of each process opening posterolaterally, and sloping inward towards sharp Y-shaped valley. Bullar lobes: large, calcified and almost as long as broad, sloping anteromesially to sharp, longitudinal groove in anterior half; pointed posteriorly.

*Sex.* Without female gonopores; penes calcified around perimeter.

*Allotype Female*

Specimen exhibiting secondary sexual characteristics of reproductively active female (see Horwitz 1988), and with 28 orange eggs, 2.0 × 1.5 mm in diameter). As for Holotype Male except:

*Cephalon.* Rostrum 0.11 × OCL, extending to junction of distal and penultimate segments of antennal peduncle. Antennal flagellum 1.00 × OCL; antennal scale 0.09 × OCL, 0.34 × as wide as long, occupying approximately one-sixth of scale length. Inner antennular flagellum 0.58 × as long as outer with outer 0.32 × OCL. 3rd maxilliped with raised mesioventral corner of coxopodite (with 2 apical tubercles); ischium with carina but not granulate along length; exopodite 0.12 × as long as ischium.

*Carapace.* 0.85 × as wide as deep; areola 0.36 × as wide as long.

*Abdomen.* TAL 1.16 × OCL.

*Tail Fan.* Telson with lateral edges straight and parallel to caudolateral corner; one caudolateral corner produced to a small spine, the other spineless. Outer ramus with 3 or 4 extra dorsomesial spines along suture and 2 or 3 extra spines dorsolaterally; outer ramus with only one spine on caudolateral corner (of both rami). Inner ramus ovoid, with spine at caudolateral corner; uropodal peduncle with a tuft of small setae.

*Chelae.* Left chela small, elongate and presumed regenerating. Right chela elongate and largely asetose; DACL/PROPL, 0.54; PROPW/PROPL, 0.45; PROPD/PROPL, 0.27; PROPL/OCL, 0.93; as for isomorph of Holotype Male except: 13 tubercles along dorsal edge of the propodus; cutting edge of propodal finger with 4 teeth in proximal third followed by small scale setae along edge to tip; cutting edge of dactyl with 2 teeth proximally followed by small scale setae to tip. Propodal finger with tufts of small setae arising from punctations (which are arranged in rows).

*Sex.* Without male gonopores but with huge, open female gonopores (ovoid, 1.3 × 0.7 mm diameter).

*Morphological variation.* The species displays some considerable morphological variation and some may be attributable to geographical location. The mesioventral corner of the coxopodite is tuberculate on individuals from Burnie Park, Shorewell Creek, but at both Romaine and Cooee creeks it is bluntly spined. The interan-

tennal spine from Romaine and Cooee creeks is clearly triangular and pointed, but at Shorewell Creek it is bluntly rounded with either convex or concave lateral edges. The exopodite of the third maxilliped is absent on individuals from Romaine Creek and extremely short on those from Cooee Creek; Shorewell Creek individuals generally have a short shaft-like stump up to 0.2 times as long as the ischium.

The suborbital angle ranges from about 80° to about 130°; the ventrolateral surface of the ischium can be tuberculate or lumpy not smooth (see Holotype). The individual from Cooee Creek had a spined rostrum which was not upturned.

*Relationship to other species.* When applied to the key to species in the genus *Engaeus* given in Horwitz (1990), *E. yabbimunna* terminates at couplet 28 with *E. tayatea* Horwitz. It can be distinguished from this species by the nature of the chela; whilst those of *E. tayatea* have tuberculate propodal palms with tufts of bristle setae, *E. yabbimunna* has a smooth and asetose propodal palm. It is readily distinguished from *E. fossor* (Erichson) by the presence of only one row of tubercles on the dorsal surface of the propodus (instead of two rows as in *E. fossor*), by the form of the rostrum and rostral carina, and by the shorter antennal flagella. Its phylogenetic affinities are unclear in spite of sharing several morphological similarities with the four species in couplets 27 and 28 (*E. fossor*, *E. strictifrons* (Clark), *E. tayatea* and *E. fultoni* Smith & Schuster; three of these occur in the western Bassian region with *E. yabbimunna*).

*Etymology.* The specific epithet was recommended by members of the Northwest Coast Aboriginal Language Programme in Burnie and means "little claw".

*Life history notes.* LM, 25.7 mm OCL; LRF, 26.0 mm OCL; SRF, 23.2 mm OCL; LNRF, 15.6 mm OCL. Berried females were collected in early December 1992; no females carrying larvae were found, suggesting that eggs had just been extruded and/or were in the early phases of developing. In fact a predominance of berried females was found at sites then (of eight adults found at the type locality, six were berried females). Most berried females were returned to their burrows to avoid depleting the population.

*Ecology.* The species has been found sympatrically with *E. fossor* (at the type locality) and is likely to occur in the same creek systems as another parastacid, *Astacopsis gouldi* Clark. No microhabitat separation has been discerned between the *Engaeus* species.

*E. yabbimunna* occupies burrows in the flood beds of creeks dominated by tree ferns, in burrows next to creeks, in seepages dominated by tea tree and with a ground cover of ferns, and well above creeks in burrows on the creek bank or slopes of the gully. Soils in these habitats ranged from brown to orange-red clay loams, or contained a high level of organic matter. Vegetation was typical of wet gullies, with *Acacia melanoxylon* dominant in the over-story. Burrow structure depended on the type of habitat and depth to water table and seemed typical of other members of this genus.

So far the species has not been found from habitats where native vegetation no longer exists (see below).

*Distribution and conservation.* Previous searches for burrowing freshwater crayfish in Tasmania have been extensive and detailed (see Horwitz, 1990; Richardson, unpublished data), and have revealed for northern Tasmania some well defined distributions. *E. fossor* for instance has a broad range across northern and western Tasmania, as do *E. cisternarius* and *E. lengana* (Horwitz, 1990). The fact that *E. yabbimunna* has until now escaped detection is evidence that some species are found locally and not over a broad area.

Collation of all data on the distribution of burrowing freshwater crayfish within about 10 km of Burnie has produced a distribution map (Fig. 2). Within the Burnie area itself eight sites were investigated. Many burrows of *E. yabbimunna* were found at the Shorewell Creek and Romaine Creek sites where flood bed and seepage areas were relatively undisturbed. Only one burrow was found at the Cooee Creek site where the creek was receiving sediment from its western side (industrial activity) and used by cattle on its eastern side. Further down Cooee Creek the original vegetation has been replaced by willows and no burrows were found. Other parts of Shorewell Creek were searched to no avail, including an area downstream of the old dump, and in the upper reaches adjacent to a sports oval; at both localities riparian vegetation had been completely removed. Parts of Shorewell Creek and Romaine Creek which have been landscaped (where vegetation has been removed and the creek channelized, for instance) were similarly devoid of burrows. These data suggest that:

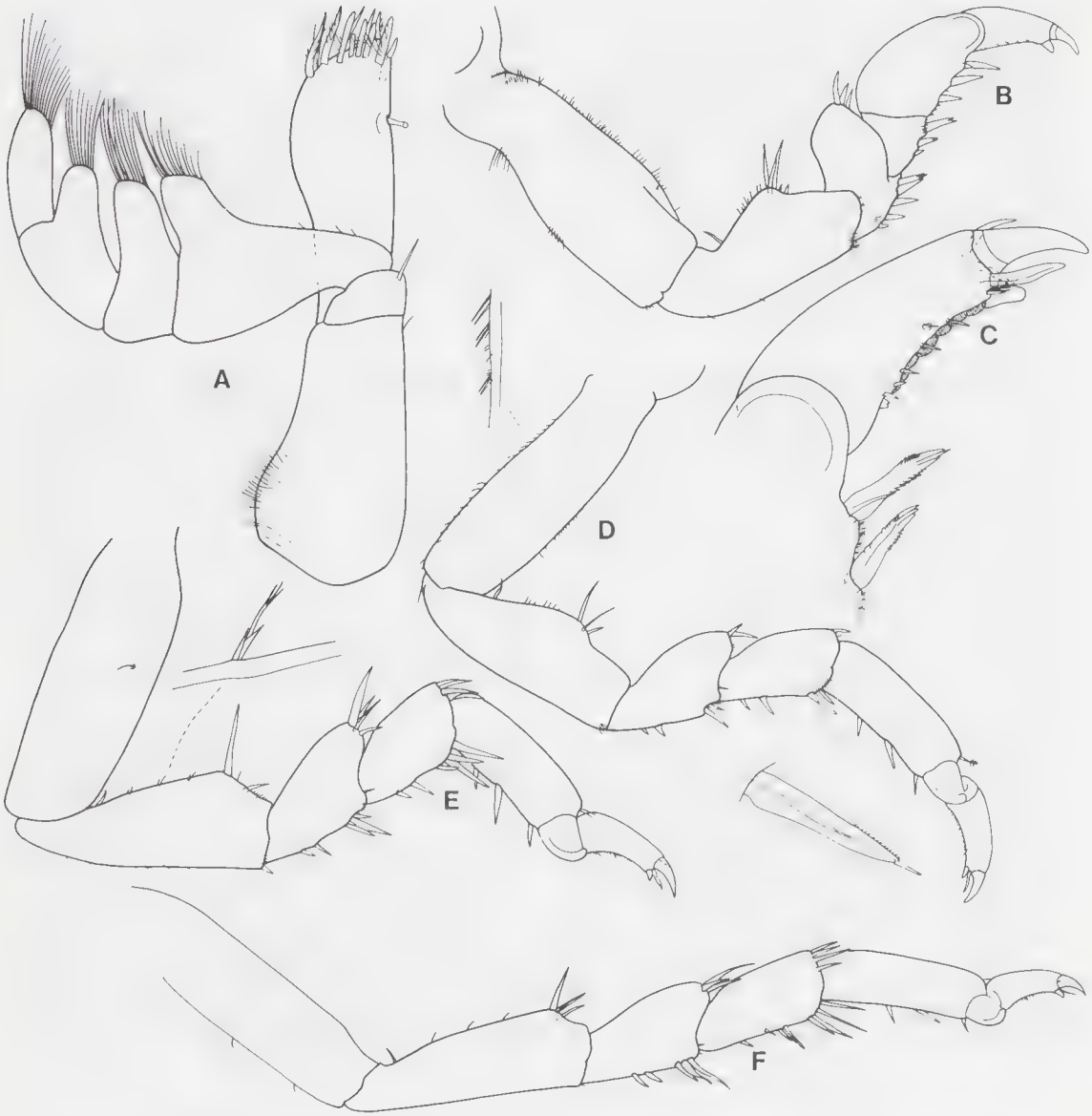


Figure 28. *Cercosphaera coloura* sp. nov. All figs paratype, SAM C5544. A, maxilliped; B, pereopod 1; C, pereopod 1, dactylus; D, pereopod 2; E, pereopod 6; F, pereopod 7.

134°36.60′E) 22 Apr 1985, 16 m, *Cystophora*, S. Shepherd and G.C.B. Poore, NMV J36937 (♂ imm. 7.8 mm).

Paratypes. SA, Pearson I., Investigator Group, 9 Jan 1969, 50 m, coarse gravel, S.A. Shepherd, (SAM C5544) (♂ imm. 6.8 mm). SA, Stokes Bay, off Kangaroo I. (35°37′S, 137°12′E) 4 Mar 1978, 7 m, mixed algae on vertical rock, I. Loch, AM P41146 (♂ juv 7.3 mm). Vic, northwest side of Henty Reef, Mounts Bay, Apollo Bay (38°47.0′S, 143°40.5′E) 18 m, red algae on boulder, R.T. Springthorpe and P.B. Berents, AM P41376 (2 mancas).

*Description of male.* Body about 1.8 times as long as wide, widest at pereonites 2–5; dorsal surface covered in rounded low nodules; lateral margin of pereonites 2–7 with nodules forming more distinct carinate ridge; large sublateral and submedian tubercles present on pereonite 4 and prominent sublateral tubercle on pereonite 5;

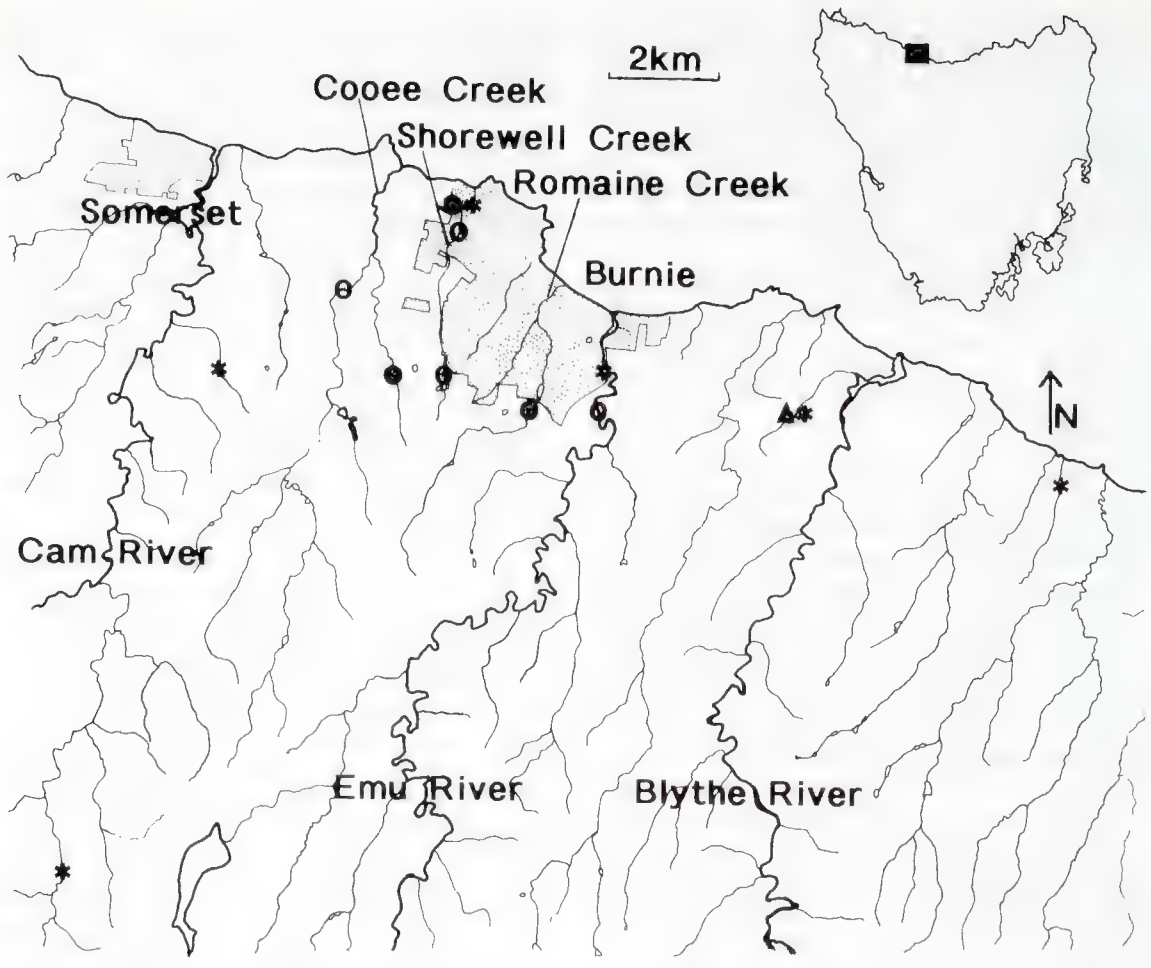


Figure 2. Distribution of *Engaeus yabbimunna* (closed circles) around Burnie (with urban area stippled) in northern Tasmania, showing the main water courses in the region, known localities of other species (*E. fossor* asterisk, *E. disjuncticus* closed triangle), and locations where searching revealed no burrows of freshwater crayfish (open circles).

i) *E. yabbimunna* may have a restricted distribution in the Burnie area and may be confined to the three creek systems from which it has been found; and

ii) populations of *E. yabbimunna* may have been eliminated by human activities in parts of the Burnie area.

The restricted distribution hypothesis is supported by the presence of only *E. fossor* at localities surrounding the three creeks, and the failure to find *E. yabbimunna* elsewhere during extensive surveys for *Engaeus* (see above). Alternatively, there is always the (albeit remote) chance that the species will occur elsewhere in northern Tasmania. For instance, the enigmatic *E. disjuncticus*, so named in Horwitz (1990) because of its disjunct populations over one hundred kilometres apart, has recently been found in the Burnie area (Richardson, pers. comm.; Fig. 2).

Even given this possibility, *E. yabbimunna* should be regarded as neither widespread nor common. Accordingly, and given that threatening processes can be identified, the species should be considered threatened and steps should be taken to consolidate knowledge on its ecology and manage its known populations appropriately.

**Acknowledgements**

Bill Walker (Burnie City Council) found the species and referred specimens to Alastair Richardson (Zoology Department, University

of Tasmania); I thank both of them for their continued interest in the species. Jacqueline Courtenay inked the drawings and compiled the distribution map.

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Memoirs of the Museum of Victoria 54(2): 447–459 (1994)

# NEW SPECIES AND NEW RECORDS OF *ECNOMUS* MCLACHLAN (TRICHOPTERA: ECNOMIDAE) FROM INDONESIA

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**Abstract**

Cartwright, D.I., 1994. New species and new records of *Ecnomus* McLachlan (Trichoptera: Ecnomidae) from Indonesia. *Memoirs of the Museum of Victoria* 54: 447–459.

Descriptions and keys are provided for males of ten species of *Ecnomus* including five new species from Kalimantan and three from Sulawesi. *Ecnomus forcipatus* Mosely, 1932 and *E. puntung* Cartwright, 1992 are also recorded from South Sulawesi. Females of eight species are figured but only one, *E. puntung*, is associated with certainty with a male. The remainder are designated *Ecnomus* species E to K. *Ecnomus retusus* sp. nov. and *E. gapit* sp. nov. have fork 1 absent in the anterior wing in males; females of *Ecnomus* sp. K also have fork 1 absent. This is the first known documentation of aberrant wing venation in the genus.

## Introduction

Twelve species of *Ecnomus* have been described previously from the Indonesian islands of Sumatra, Java and Sulawesi (Mosely, 1932; Ulmer, 1951; Cartwright, 1992). The genus has not been recorded previously from Kalimantan (Indonesian Borneo), but one species has been described from the adjacent Malaysian state, Sarawak (Kimmins, 1955). The biogeography and phylogeny of the genus *Ecnomus* in the south-eastern Asian-Australian region will be considered at a later date when more species have been described, especially from other areas of Indonesia and from Papua New Guinea.

Species are best identified by differences in male and female genitalia, which usually requires clearing the abdomen in potassium hydroxide. Males and females can seldom be associated positively unless collected in copula or bred through from larvae.

Depositories for specimens are abbreviated as follows:

The Natural History Museum, London (BMNH), Museum of Victoria, Melbourne (NMV), National Natuurhistorisch Museum, Leiden (RMNH), Zoologisch Museum, Universiteit van Amsterdam (ZMA). CT- numbers refer to the notebook of the author.

## *Ecnomus* McLachlan

*Ecnomus* McLachlan, 1864: 30.

*Type species. Philopotamus tenellus* Rambur, 1842 (by original designation).

*Diagnosis* (revised after Neboiss, 1977). Maxillary palpi with segment 1 short, segments 2, 3 and 4 successively slightly longer than preceding segment, segment 5 about as long as all other segments together. Mesoscutum and scutellum each with a pair of rounded warts. Anterior wings with R1 forked at apex, apical forks 1 (absent in two species), 2, 3, 4 and 5 present, fork 1 short; discoidal, median and thyridial cells present. Posterior wings slightly narrower than anterior wings; forks 2 and 5 present; discoidal cell absent. Tibial spurs 3:4:4.

*Remarks. Ecnomus* females usually have short abdominal segments 9 and 10 but there is at least one exception: *Ecnomus* sp. A from North Sulawesi (Cartwright, 1992).

### Checklist of Indonesian species of *Ecnomus*

*Ecnomus asciatus* Ulmer, 1951
*E. bengkok* sp. nov.
*E. buntak* Cartwright, 1992
*E. forcipatus* Mosely, 1932
*E. furcatus* Ulmer, 1951
*E. gada* sp. nov.
*E. gapit* sp. nov.
*E. kelung* sp. nov.
*E. obtusus* Ulmer, 1951
*E. pseudotenellus* Ulmer, 1951
*E. puntung* Cartwright, 1992
*E. retusus* sp. nov.
*E. robustior* Ulmer, 1951
*E. seluk* sp. nov.
*E. serratus* Ulmer, 1951

*E. singkarakensis* Ulmer, 1951
*E. tang* Cartwright, 1992
*E. tegap* sp. nov.
*E. tipis* Cartwright, 1992
*E. tjurupensis* Ulmer, 1951
*E. yuleae* sp. nov.

**Key to males of species of *Ecnomus* from Sulawesi and Kalimantan**

1. Anterior wing with fork 1 absent (Fig. 1) ..... 2
— Anterior wing with fork 1 present ..... 3
2(1). Inferior appendages with subapical notch (Figs 2, 3) ..... *E. retusus* sp. nov.
— Inferior appendages without subapical notch (Figs 4, 5) ..... *E. gapit* sp. nov.
3(1). Superior appendages in lateral view very short, length about same as width, not dilated apically (Cartwright, 1992; Fig. 1) ..... *E. buntak* Cartwright
— Superior appendages in lateral view long, length greater than width, usually dilated apically (Figs 6, 8) ..... 4
4(3). Superior appendages in lateral view with length about 1.3 × width, truncate apically (Fig. 6) ..... *E. puntung* Cartwright
— Superior appendages in lateral view with length greater than twice width, rounded apically (Figs 8,10) ..... 5
5(4). Inferior appendages in ventral view short, straight and robust, length about 3 × width (Fig. 9) ..... *E. tegap* sp. nov.
— Inferior appendages in ventral view long, slender in apical half, usually with apices inflexed, length greater than 3.5 × width (Figs 11, 13) ..... 6
6(5). Superior appendages with ventrally directed projection on basiventral margin (Fig. 10) ..... *E. bengkok* sp. nov.
— Superior appendages without ventrally directed projection on basiventral margin (Figs 12) ..... 7
7(6). Superior appendages in lateral view robust, broadbased, length about 2.5 × width (Fig. 12) ..... 8
— Superior appendages in lateral view long, slender, dilated apically, length greater than 3 × width (Figs 16, 18) ..... 9
8(7). Inferior appendages in ventral view dilated apically (Fig. 13) ..... *E. gada* sp. nov.
— Inferior appendages in ventral view tapered apically (Fig. 15) ..... *E. yuleae* sp. nov.
9(7). Inferior appendages in lateral view with mesal projection protruding above dorsal margin; parameres simple (Figs 16, 18) ..... 10
— Inferior appendages in lateral view without mesal projection protruding above dorsal margin; parameres branched (Fig. 20) ..... 11
10(9). Inferior appendages broadest in basal half, slender and inflexed strongly in distal half (Figs 16, 17) ..... *E. forcipatus* Mosely
— Inferior appendages similar width along whole length, weakly inflexed in distal half (Figs 18, 19) ..... *E. kelung* sp. nov.

11(9). Inferior appendages in lateral view slender, tapering slightly apically (Cartwright, 1992; Fig. 7) ..... *E. tipis* Cartwright

— Inferior appendages in lateral view robust, broadest near middle, tapering slightly apically (Fig. 20) ..... 12

12(11). Inferior appendages in ventral view with digitiform mesal projection (Cartwright, 1992; Fig. 6) ..... *E. tang* Cartwright

— Inferior appendages in ventral view without digitiform mesal projection (Fig. 21). ..... *E. seluk* sp. nov.

***Ecnomus retusus*** sp. nov.

Figures 1–3

*Type material.* Holotype male, East Kalimantan, Mahakam River, 250 km W of Samarinda, 10 Mar 1991, C. Yule (NMV T-14304).

Paratypes: 2 males, same data as holotype (genitalia prep. CT-193 figured, NMV); 1 male, Long Hubungan, Mahakam River, 250 km W of Samarinda, 10 Mar 1991, C. Yule (NMV); 1 male, Camp Prampus, Kelian River trib. of Mahakam River, 250 km W of Samarinda, light trap, 31 Mar 1991, C. Yule (NMV).

*Description.* Male. Wings fawn to pale brown with paler irrorations, venation characteristic of genus except fork 1 absent on anterior wing (Fig. 1). Ventrolateral processes of segment 10 very long, slender with 3 small setae apically. Superior appendages in lateral view long and slender, length about 4 × width, narrowed in the middle (Fig. 2), with field of mesally-directed spiny setae apically; inferior appendages in ventral view long and slender, length about 4 × width, with a small incision subapically (Fig. 3), in lateral view long and straight, length about 3.5 × width; in lateral view parameres robust, dilated or bulbous apically (Fig. 2); phallus with single spine subapically (Figs 2, 3).

Female unknown.

Length of forewing: male 3.3–3.7 mm.

***Etymology.*** Latin, notched at the apex, referring to the shape of the inferior appendages.

*Distribution.* East Kalimantan (Indonesia).

*Remarks. Ecnomus retusus* and *E. gapit* sp. nov. are the only known species of *Ecnomus* lacking fork 1 in the anterior wing. *Ecnomus retusus* has a distinctive subapical notch on the inferior appendages. The phallus has a single large spine embedded subapically, which has also been recorded in the Australian species *E. wellsae* Cartwright.

***Ecnomus gapit*** sp. nov.

Figures 4, 5

*Type material.* Holotype male, East Kalimantan, Kelian River trib. of Mahakam River, 250 km W of Samarinda, light trap, 4 Sep 1992, C. Yule (NMV T-14309; specimen CT-216 figured).

*Description.* Male. Wings fawn with some paler irrorations, venation characteristic of genus except fork 1 absent on anterior wing as for *E. retusus*. Ventrolateral processes of segment 10 very short, rounded with 3 short setae apically. Superior appendages in lateral view robust, length about twice width, narrowed near middle (Fig.4), apices with dense field of mesally directed spiny setae; inferior appendages in ventral view slender, broadest near base, apices inflexed (Fig. 5), and dorsoventrally flattened, in lateral view straight, slender, tapering apically; parameres in lateral view straight and slender; phallus with acute apex (Fig. 4).

Female unknown.

Length of forewing: male 3.9 mm.

*Etymology.* Indonesian, meaning tweezers or pincers, referring to the shape of the inferior appendages.

*Distribution.* East Kalimantan (Indonesia).

*Remarks. Ecnomus gapit* is known from only one male specimen which, like *E. retusus*, lacks fork 1 in the anterior wings. It can be distinguished by the dorsoventrally flattened apices on the inferior appendages.

***Ecnomus puntung*** Cartwright

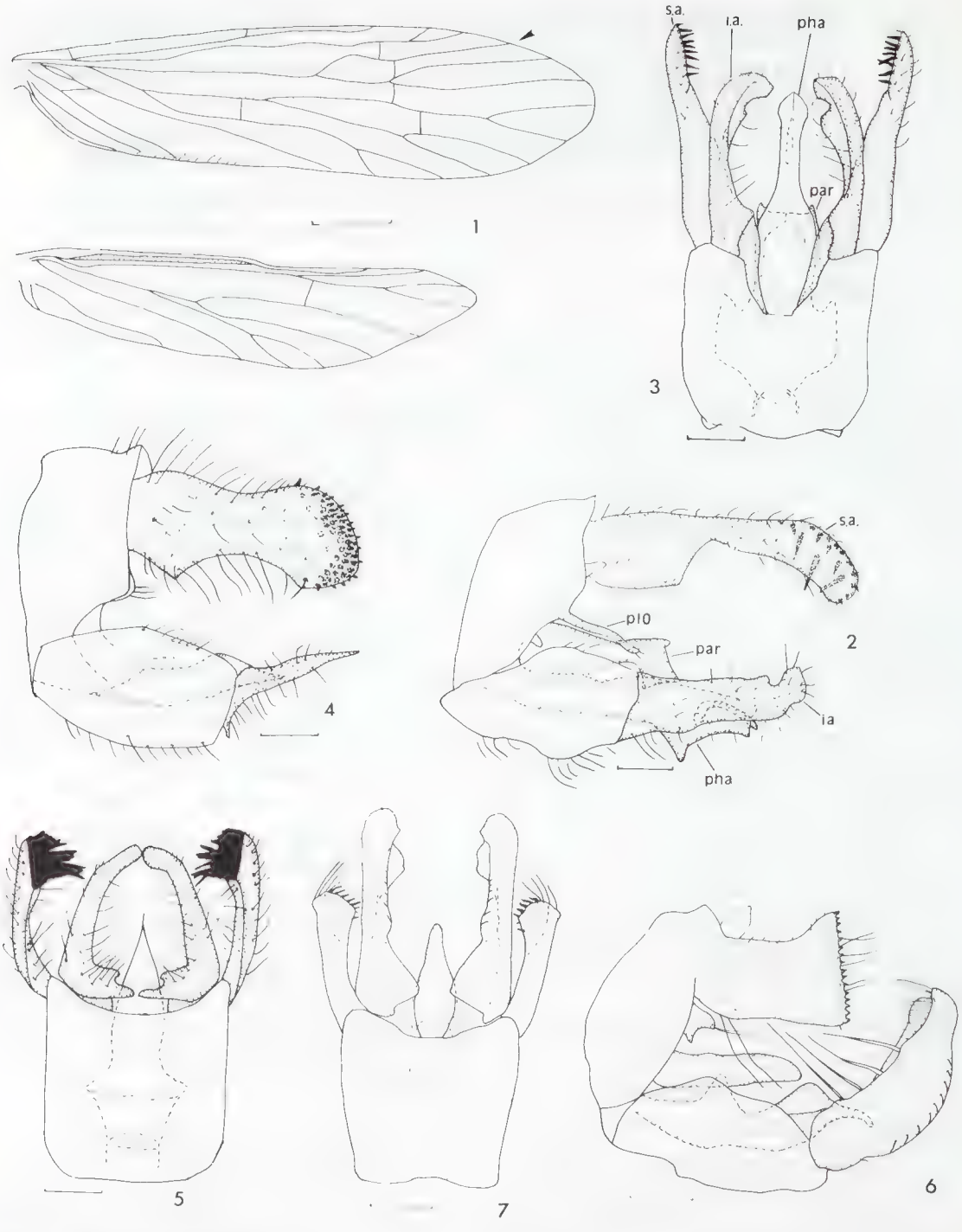
Figures 6, 7, 22, 23

*Ecnomus puntung* Cartwright 1992: 102, figs 3–4.
*Ecnomus* sp. C (female) 1992: 107, figs 13–14.

*Material examined.* Holotype male, Sulawesi Utara, Dumoga Bone National Park, Edwards Camp near Tumpah River, 650 m, 00°35′ 123°51′E, MV light, 22 May 1985, A. Wells (NMV T-10727).

Paratypes, 20 males, same data as holotype (NMV, RMNH, ZMA).

*Additional material.* Sulawesi Tenggara, many males,




Figures 1–7: *Ecnomus* spp. Males. 1–3, *Ecnomus retusus* sp. nov.; 1, wings; 2, genitalia, lateral view; 3, genitalia, ventral view; 4, 5, *Ecnomus gapit* sp. nov., genitalia; 4, lateral view; 5, ventral view; 6, 7, *Ecnomus puntung* Cartwright, genitalia; 6, lateral view; 7, ventral view. Abbreviation: i.a., inferior appendages; par, parameres; pha, phallus; p10, ventrolateral processes of segment 10; s.a., superior appendages. Scale lines: 0.5 mm (Fig. 1), 0.1 mm (Figs 2–7).

females, many sites, Oct-Nov 1989, R. de Jong and J. Huisman (RMNH). List of localities available from author.

*Description* (revised after Cartwright, 1992). Wings fawn to pale brown with paler irrorations.

Male. Ventrolateral processes of segment 10 short, bilobed with 3 short setae apically. Superior appendages in lateral view short and broad, length about 1.3 × width, apices dilated and truncate (Fig. 6), with field of mesally-directed spiny setae; inferior appendages in ventral view length about 3 × width, broadest near base, with broad mesal lobe dorsally (Fig. 7), in lateral view length about 3 × width, broadest in middle, with several long hair-like setae dorsally (Fig. 6) and series of grooves ventrally (Figs 6, 7); parameres straight and robust; phallus extended into long, slender apical projection (Fig. 6).

Female. Ventral plates with shallow concavity near mesal margin in middle, length about 1.5 × width, apices smoothly rounded (Figs 22, 23).

Length of forewing: male 3.7–4.4mm; female 3.5–4.5 mm.

*Distribution.* North and South Sulawesi (Indonesia).

*Remarks. Ecnomus puntung* is the commonest species of *Ecnomus* collected from Sulawesi. The male can be readily distinguished by the truncate superior appendages. The female has a distinctive concavity on each ventral plate.

***Ecnomus tegap*** sp. nov.

Figures 8, 9

*Type material.* Holotype male, East Kalimantan, Mahakam River, 250 km W of Samarinda, 10 Mar 1991, C. Yule (NMV T-14310).

Paratypes: male, same data as holotype (genitalia prep. CT-194 figured; NMV); 2 males, Long Hubungan, Mahakam River, 250 km W of Samarinda, 10 Mar 1991, C. Yule (NMV).

*Description.* Male. Wings fawn with some paler irrorations, venation characteristic of genus. Ventrolateral processes of segment 10 long, slender with 3 small setae apically. Superior appendages in lateral view long and robust, length about twice width, tapering slightly apically, with small digitiform projection mesally (Fig. 8), field of mesally-directed spiny setae apically; inferior appendages in ventral view straight, robust, subrectangular, length about 3 × width (Fig. 9), in lateral view robust, length about twice width, with broad projection apically; parameres absent; phallus with small digitiform projection dorsally (Fig. 8).

Female unknown.

Length of forewing: male 3.4–3.7 mm.

*Etymology.* Indonesian, *tegap* meaning robust, referring to the shape of the inferior appendages.

*Distribution.* East Kalimantan (Indonesia).

*Remarks. Ecnomus tegap* can be distinguished from other Indonesian species by the robust appearance of both the superior and inferior appendages.

***Ecnomus bengkok*** sp. nov.

Figures 10, 11

*Type material.* Holotype male, Sulawesi Tenggara, N slope Gunng Watuwila, 250 m, light, 19 Oct. 1989, R. de Jong and J. Huisman, (RMNH JS 8918), Mokowu camp, Sg. Mokowu (genitalia prep. CT-206 figured, RMNH).

*Description.* Male. Wings pale fawn. Ventrolateral processes of segment 10 straight with 3 small setae apically. Superior appendages in lateral view long, length about 3 × width, a digitiform process present on ventral margin near base (Fig. 10), with a field of mesally directed spiny setae apically; inferior appendages in ventral view long and slender, length about 6 × width, apices slightly inflexed and with bifid appearance especially in apical view (Fig. 11), in lateral view long and straight, length about 4 × width; in lateral view parameres simple, straight and robust; phallus with upper apical angle extended into a slender point (Fig. 10).

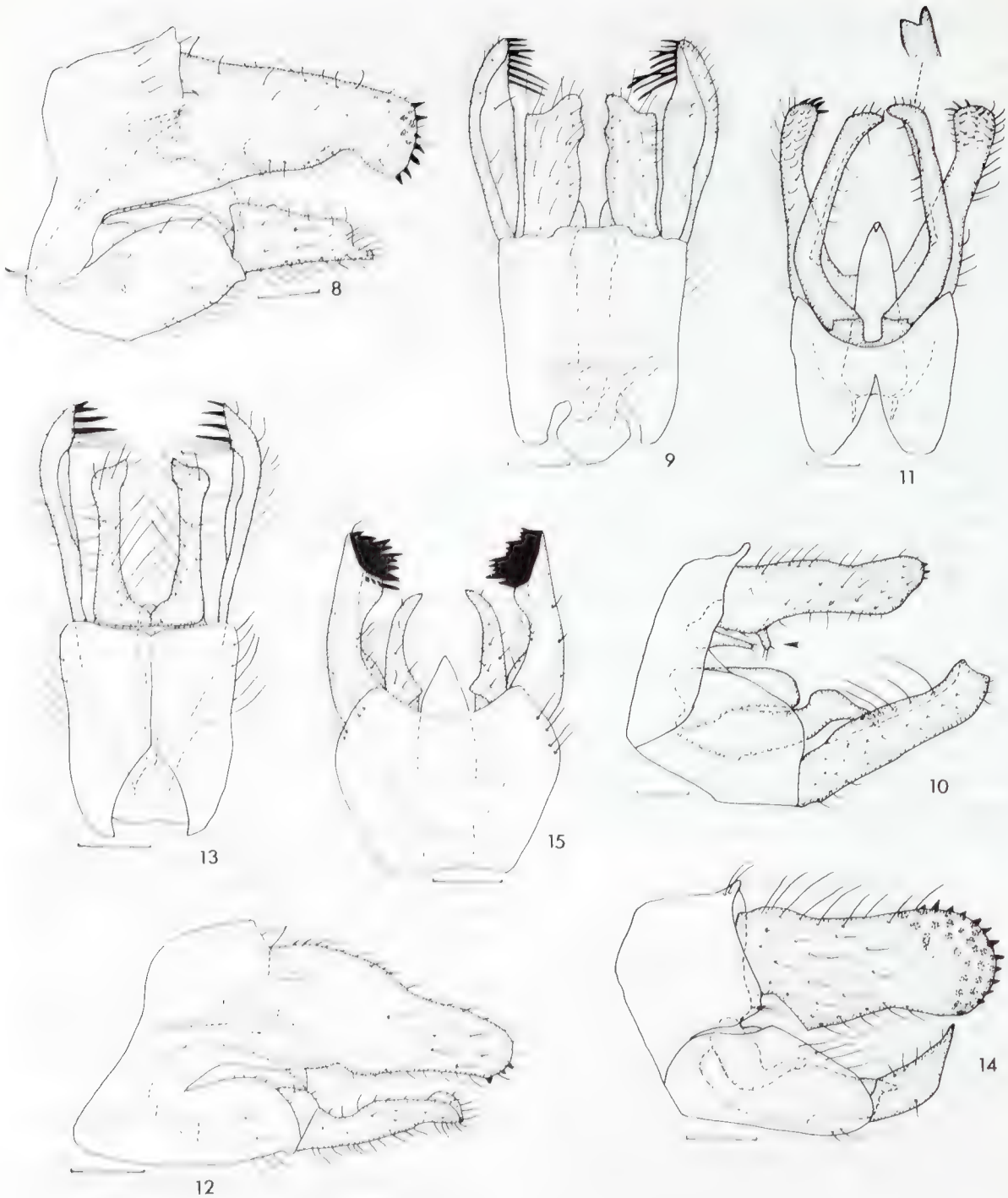
Female unknown.

Length of forewing: male 3.8 mm.

*Etymology.* Indonesian, *bengkok* meaning somewhat bent or crooked, referring to the shape of the inferior appendages.

*Distribution.* South Sulawesi (Indonesia), known from type locality only.

*Remarks.* The single male specimen resembles two Australian species, *E. turgidus* Neboiss and *E. digrutus* Cartwright, and *E. penjabi* Schmid from Pakistan, in having a ventral projection on the superior appendages. It can be distinguished from these three species by the lack of a small projection on the inferior appendages as in the two Australian species and the robust superior and inferior appendages compared with *E. penjabi.*




Figures 8–15: *Ecnomus* spp. Male, genitalia. 8, 9, *Ecnomus tegap* sp. nov. 8, lateral view; 9, ventral view; 10, 11, *Ecnomus bengkok* sp. nov.; 10, lateral view; 11, ventral view; 12, 13, *Ecnomus gada* sp. nov. 12, lateral view; 13, ventral view; 14, 15, *Ecnomus yuleae* sp. nov.; 14, lateral view; 15, ventral view. All scale lines 0.1 mm.

### ***Ecnomus gada*** sp. nov.

Figures 12, 13

*Type material.* Holotype male, East Kalimantan, Long Hubungan, Mahakam River, 250 km W of Samarinda, 10 Mar 1991, C. Yule (NMV T-14314).

Paratypes: 2 males, same data as holotype (NMV); male, East Kalimantan, Mahakam River, 250 km W of Samarinda, 10 Mar 1991, C. Yule (genitalia prep. CT-192 figured, NMV); male, East Kalimantan, Kelian River trib. of Mahakam River, 250 km W of Samarinda, light trap, 30 Jun 1992, C. Yule (NMV).

*Description.* Male. Wings fawn with some paler irrorations. Ventrolateral processes of segment 10 long, slender, with 3 small setae apically. Superior appendages in lateral view long and robust, length about twice width, tapered slightly apically (Fig. 12), with a field of spiny setae apically; inferior appendages in ventral view long and slender, length about 3.5 × width, slightly dilated subapically (Fig. 13), in lateral view straight and slender, length about 4 × width; parameres absent; phallus slightly swollen distally, tapered apically (Fig. 12).

Female unknown.

Length of forewing: male 2.8–3.1 mm.

*Etymology.* Indonesian, *gada* meaning club, referring to the shape of the inferior appendages.

*Distribution.* East Kalimantan (Indonesia).

*Remarks. Ecnomus gada* can be distinguished from other Indonesian species by the robust superior appendages, slender inferior appendages and lack of parameres.

### ***Ecnomus yuleae*** sp. nov.

Figures 14, 15

*Type material.* Holotype male, East Kalimantan, Kelian River trib. of Mahakam River, 250 km W of Samarinda, Light trap, 30 Jun 92, C. Yule (NMV T-14319, specimen CT-218 figured).

*Description.* Male. Wings fawn with some paler irrorations. Ventro-lateral processes of segment 10 reduced to inconspicuous swellings with 3 small setae apically. Superior appendages in lateral view robust, length about 2.5 × width (Fig. 14), apices with dense field of mesally directed spiny setae; inferior appendages laterally compressed, in ventral view slender, length about 3.5 × width, broadest near base (Fig. 15), in lateral view broadest near middle, tapered apically; parameres in lateral view short and slender; phallus with apex extended into a short projection (Fig. 14).

Female unknown.

Length of forewing: male 3.3 mm.

*Etymology.* The species is named for Cathy Yule (collector).

*Distribution.* East Kalimantan (Indonesia).

*Remarks.* The single male specimen can be distinguished from other Indonesian species by the simple, laterally compressed inferior appendages and robust superior appendages.

### ***Ecnomus forcipatus*** Mosely

Figures 16, 17

*Ecnomus forcipatus* Mosely 1932: 4, figs 11-13.

*Type material.* Holotype male, Taiping, Perak, F.M.S., (West Malaysia), Apr 1912, J. Henderson (BMNH).

Paratype male, same data as holotype (BMNH). Types not seen.

*Material examined.* Sulawesi Tenggara, 1 male, Desa Aopa, 50 m, at light, 27 Oct 1989, R. de Jong and J. Huisman (RMNH JS 8928), (genitalia prep. CT-207 figured, RMNH).

*Description* (revised after Mosely, 1932). Male. Wings pale fawn. Ventrolateral processes of segment 10 straight, with 3 small setae apically. Superior appendages in lateral view long, straight, length about 4.5 × width (Fig. 16), with a field of mesally directed spiny setae apically; inferior appendages hairy, in ventral view, slender, apices inflexed, broadened into a swelling basally (Fig. 17), in lateral view broad basally, slender and upturned in apical half, with small rounded knob on dorsal margin; parameres robust, dilated and downturned apically; phallus mostly hidden between parameres (Fig. 16).

Female unknown.

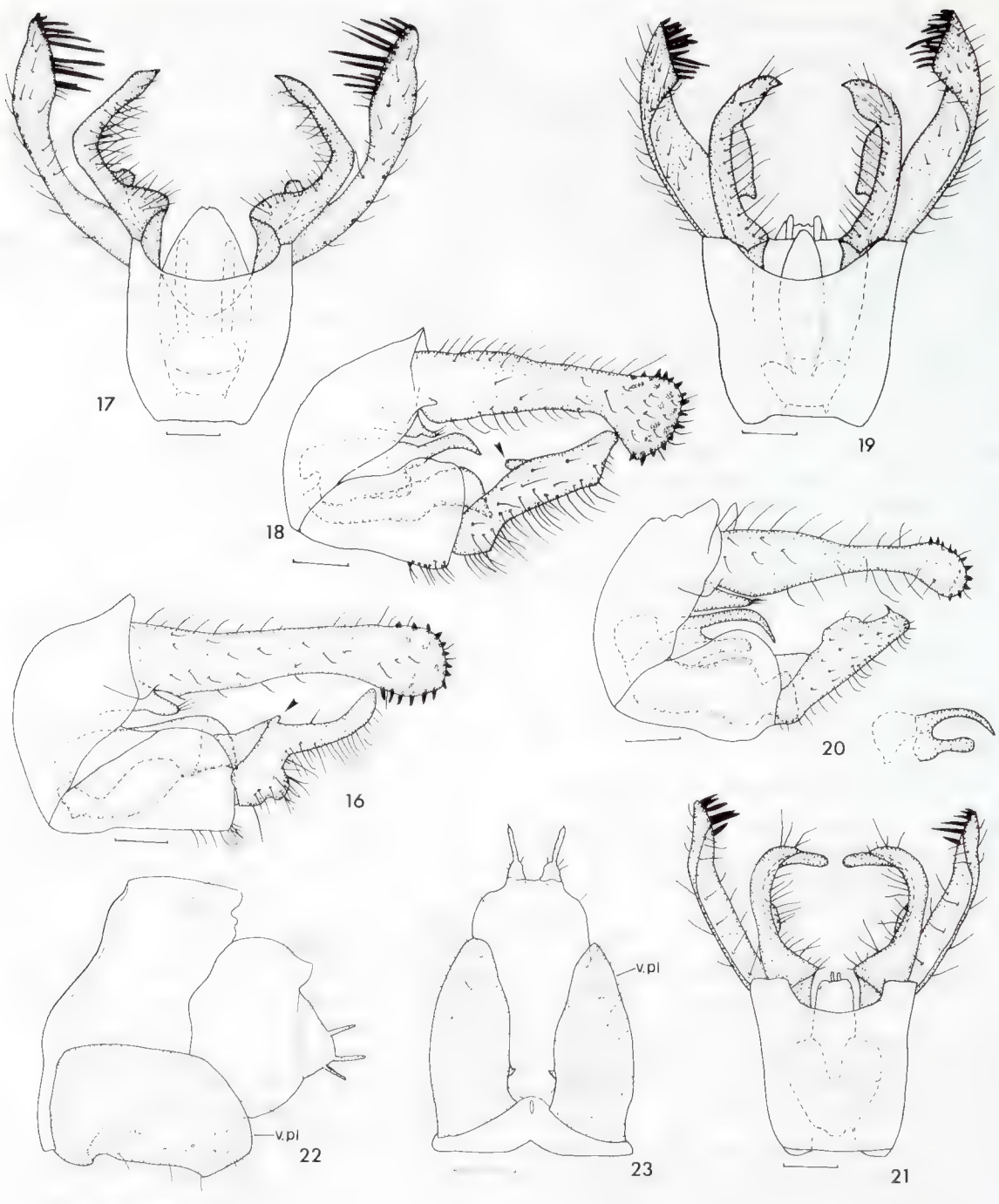
Length of forewing: male 3.8–4.0 mm.

*Distribution.* South Sulawesi (Indonesia) and Perak (West Malaysia).

*Remarks. Ecnomus forcipatus* was described originally from the Malay Peninsula (Mosely, 1932), and can be distinguished from other Indonesian species by the strongly inflexed apical half of the inferior appendages and the projection on the dorsal margin.

### ***Ecnomus kelung*** sp. nov.

Figures 18, 19




Figures 16–23: *Ecnomus* spp. genitalia. 16, 17, *Ecnomus forcipatus* Mosely, male; 16, lateral view; 17, ventral view; 18, 19, *Ecnomus kelung* sp. nov., male; 18, lateral view; 19, ventral view; 20, 21, *Ecnomus seluk* sp. nov., male; 20, lateral view and parameres lateral view; 21, ventral view; 22, 23, *Ecnomus puntung* Cartwright, female; 22, lateral view; 23, ventral view. Abbreviation: v. pl., ventral plate. All scale lines 0.1 mm.

*Type material.* Holotype male, Sulawesi Tenggara, Pulau Kabaena, Batuawu, at light, 11 Nov 1989, R. de Jong and J. Huisman (RMNH JS 8945), Sg. Lebokomea.

Paratypes: 3 males, same data as holotype (genitalia prep. CT-209 figured, RMNH); 4 males, Sulawesi Tenggara, Moramo Sg., Moramo, 200 m, at light, 16 Nov 1989, R. de Jong and J. Huisman, RMNH JS 8947 (RMNH).

*Description.* Male. Wings pale fawn. Ventrolateral processes of segment 10 short, broadbased, with 3 small setae apically. Superior appendages in lateral view long and slender, length about 3 × width, apices dilated (Fig. 18), and with field of mesally directed spiny setae; inferior appendages hairy, in ventral view, slender, length about 4 × width, with broad dorsal lobe near middle, apices pointed, slightly inflexed and with spatulate appearance (Fig. 19), in lateral view slightly upturned, length about 4.5 × width, with small dorsal projection near middle; in lateral view parameres long, slender, downcurved apically with ventral lobe; phallus slightly dilated subapically with acute apex (Fig. 18).

Female unknown.

Length of forewing: male 3.2–3.9 mm.

*Etymology.* Indonesian, *kelung* meaning bent or hollow, referring to the shape of the inferior appendages.

*Distribution.* South Sulawesi (Indonesia).

*Remarks. Ecnomus kelung* males resemble *E. tang* Cartwright and *E. tipis* Cartwright from N Sulawesi, *E. forcipatus* Mosely from the Malay Peninsula and E Kalimantan, and *E. seluk* sp. nov., in all genitalic structures, but is distingished by the spatulate shape of the inferior appendages.

### ***Ecnomus seluk*** sp. nov.

Figures 20, 21

*Type material.* Holotype male, Sulawesi Tenggara, Moramo, Sg. Moramo, 200 m, at light, 16 Nov 1989, R. de Jong and J. Huisman (RMNH JS 8947).

Paratypes: 3 males, same data as holotype (genitalia prep. CT-201 figured, RMNH).

*Description.* Male. Wings pale fawn. Ventrolateral processes of segment 10 long, straight, with 3 small setae apically. Superior appendages in lateral view long and slender, length about 4 × width, apices slightly dilated (Fig. 20), and with field of mesally directed spiny setae; inferior appendages hairy, in ventral view slender, broadest near base, apices inflexed (Fig. 21), in lateral view straight and robust, length about 3 × width, with broad dorsal lobe near middle and small apical projection; in lateral view parameres branched, with dorsal branch long and slender, downcurved apically, ventral branch straight and robust; phallus swollen subapically (Fig. 20), with two small processes apically (Fig. 21).

Female unknown.

Length of forewing: male 3.0–3.4 mm.

*Etymology.* Indonesian, *seluk* meaning curve or bend, referring to the shape of the inferior appendages.

*Distribution.* South Sulawesi (Indonesia).

*Remarks. Ecnomus seluk* males resemble *E. tang* Cartwright, *E. tipis* Cartwright, *E. kelung* and *E. forcipatus* Mosely in all genitalic structures, but can be separated by the shape of the dorsal lobe on the inferior appendages and the form of the parameres.

### ***Ecnomus*** sp. E (female)

Figures 24, 25

*Material examined.* Sulawesi Tenggara, 9 females, Pulau Kabaena, Batuawu, at light, 11 Nov 1989, R. de Jong and J. Huisman (RMNH JS 8945), Sg. Lebokomea (genitalia prep. CT-208 figured; RMNH); 2 females, Moramo, Sg. Sena, 50 m, at light, 15 Nov 1989, R. de Jong and J. Huisman (RMNH JS 8946); 1 female, Moramo, Sg. Moramo, 200 m, at light, 16 Nov 1989, R. de Jong and J. Huisman, (RMNH JS 8947).

*Description.* Female. Wings fawn to pale brown with paler irrorations. Ventral plates with length about twice width, tapered apically, apices acute (Figs 24, 25).

Length of forewing: female 3.6–4.1 mm.

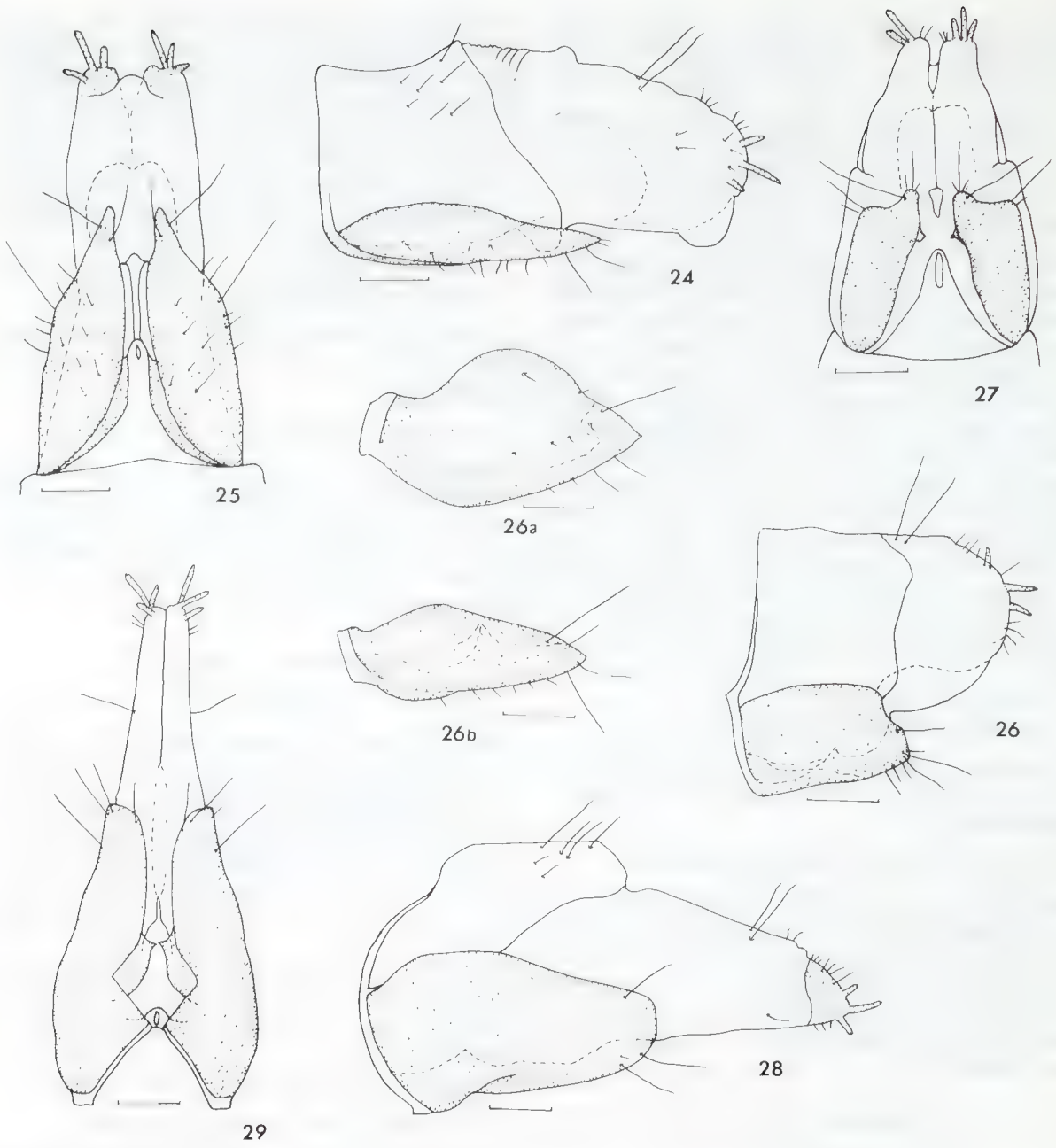
*Distribution.* South Sulawesi (Indonesia).

*Remarks. Ecnomus* sp. E has ventral plates similar to those of *Ecnomus* sp. B from North Sulawesi but with apices more acute.

### ***Ecnomus*** sp. F (female)

Figures 26, 27

*Material examined.* Sulawesi Tenggara, 6 females, Moramo, Sg. Moramo, 200 m, at light, 16 Nov 1989, R. de Jong and J. Huisman (RMNH JS 8947), (genitalia prep. CT-203 figured, CT-204 partly figured; RMNH); 1 female, Desa Aopa, 50 m, at light, 27 Oct 1989, R. de Jong and J. Huisman (RMNH JS 8928), (genitalia prep. CT-210 partly figured; RMNH).




Figures 24–29: *Ecnomus* spp., female genitalia. 24, 25, *Ecnomus* sp. E; 24, lateral view; 25 ventral view; 26, 27, *Ecnomus* sp. F; 26, lateral view; 26a, b, variations in form of ventral plate in lateral view; 27, ventral view; 28, 29, *Ecnomus* sp. G; 28, lateral view; 29 ventral view. All scale lines 0.1 mm.

*Description.* Female. Wings fawn to pale brown with paler irrorations. Ventral plates with shape variable, from sub-rectangular (Figs 26a, 26b) to more elongate, narrowed apically (Figs 26, 27).

Length of forewing: female 3.3–4.3 mm.

*Distribution.* South Sulawesi (Indonesia).

*Remarks. Ecnomus* sp. F is somewhat variable in the shape of the ventral plates, but is similar to *Ecnomus* sp. D from North Sulawesi, although lacking the strong ridge on the mesal margin of the ventral plates.

### ***Ecnomus*** sp. G (female)

Figures 28, 29

*Material examined.* Sulawesi Tenggara, 45 females, Moramo, Sg. Moramo, 200 m, at light, 16 Nov 1989, R. de Jong and J. Huisman (RMNH JS 8947), (genitalia prep. CT-202 figured; RMNH); 1 female, Moramo, Sg. Moramo, 175 m, at light, 17 Nov 1989, R. de Jong and J. Huisman, (RMNH JS 8949); 1 female, Desa Aopa, 50 m, at light, 27 Oct 1989, R. de Jong and J. Huisman, (RMNH JS 8928); 1 female, Pulau Kabaena, 1 km S Tangkeno, Sg. Lantinol, 550 m, UV-light, 9 Nov 1989, R. de Jong and J. Huisman, (RMNH JS 8940-42).

*Description.* Female. Wings fawn to pale brown with paler irrorations. Ventral plates with length about twice width, rounded apically, segment 9 laterally compressed (Figs 28, 29).

Length of forewing: female 3.5–4.4 mm.

*Distribution.* South Sulawesi (Indonesia).

*Remarks. Ecnomus* sp. G has similar genitalic characters to *Ecnomus* sp. B from North Sulawesi, but the apices of the ventral plates are more rounded and slightly truncated.

### ***Ecnomus*** sp. H (female)

Figures 30, 31

*Material examined.* East Kalimantan, 5 females, Mahakam River, 250 km W of Samarinda, 10 Mar 1991, C. Yule (genitalia prep. CT-195 figured; NMV); 28 females, Long Hubungan, Mahakam River, 250 km W of Samarinda, 10 Mar 1991, C. Yule (NMV).

*Description.* Female. Wings fawn to pale brown with paler irrorations. Ventral plates with length about 1.5 × width, tapered apically, apices rounded in lateral view (Figs 30, 31).

Length of forewing: female 3.0–3.7 mm.

*Distribution.* East Kalimantan (Indonesia).

*Remarks. Ecnomus* sp. H females can be separated from other Kalimantan females by the lack of pockets on the ventral plates as in *Ecnomus* sp. K and *Ecnomus* sp. J, and the apices of the ventral plates are less truncated than in *Ecnomus* sp. I.

### ***Ecnomus*** sp. I (female)

Figures 32, 33

*Material examined.* East Kalimantan, 1 female, Long Hubungan, Mahakam River, 250 km W of Samarinda, 10 Mar 1991, C. Yule (genitalia prep. CT-198 figured; NMV).

*Description.* Female. Wings pale brown. Ventral plates with length about equal to width, subquadrate, truncated apically (Figs 32, 33).

Length of forewing: female 4.4 mm.

*Distribution.* East Kalimantan (Indonesia).

*Remarks. Ecnomus* sp. I can be distinguished from other females by the quadrate ventral plates in lateral and ventral views.

### ***Ecnomus*** sp. J (female)

Figures 34, 35

*Material examined.* East Kalimantan, 1 female, Mahakam River, 250 km W of Samarinda, 10 Mar 1991, C. Yule (genitalia prep. CT-213 figured; NMV).

*Description.* Female. Wings pale brown with some paler irrorations. Ventral plates with length about same as width, apices rounded in lateral view, with shallow mesally facing pocket near mid-mesal margin, shallow groove basal to pocket and shallow concavity laterad to pocket (Figs 34, 35).

Length of forewing: female 4.5 mm.

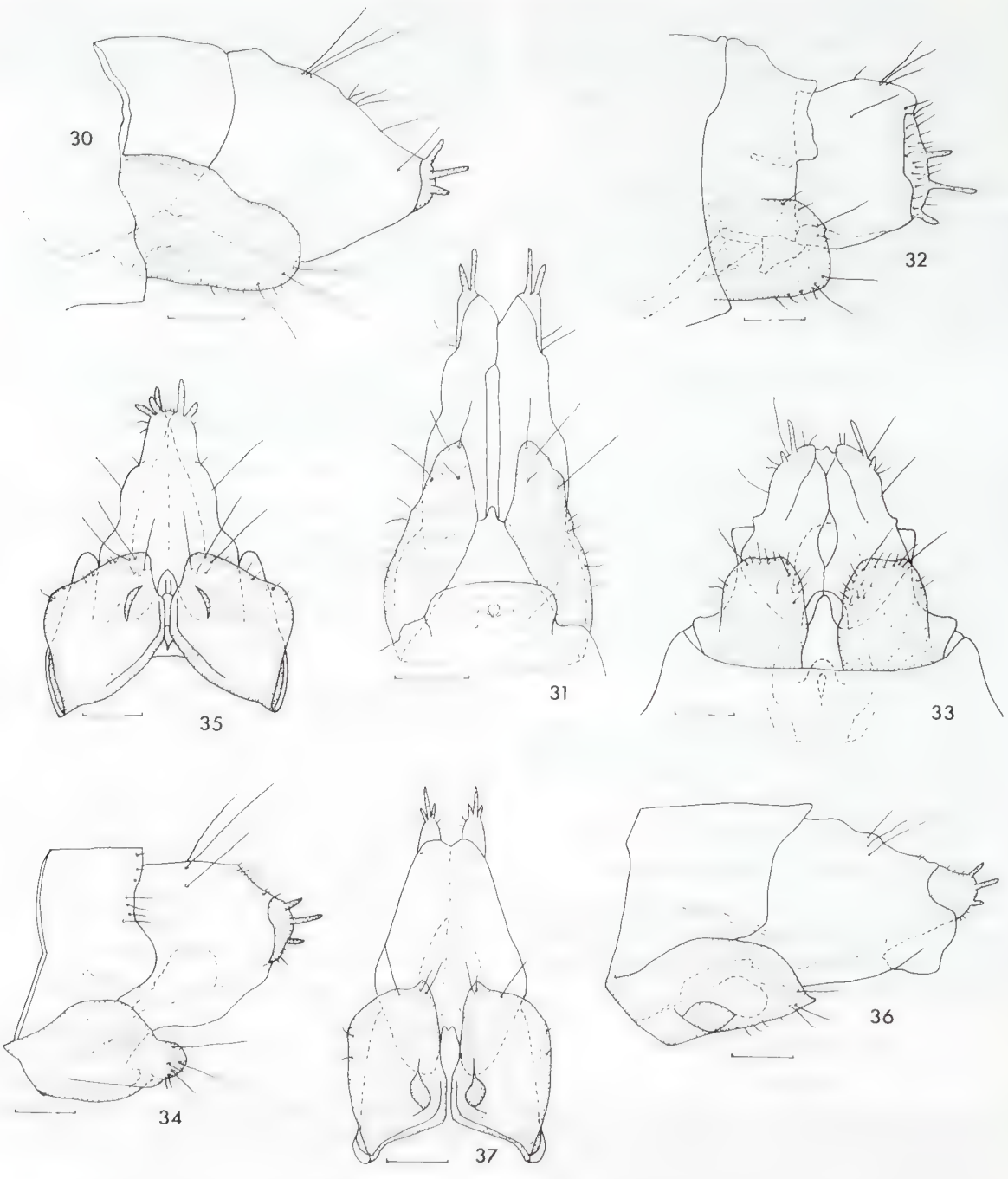
*Distribution.* East Kalimantan (Indonesia).

*Remarks.* The single female specimen is similar to *Ecnomus* sp. K from East Kalimantan in having a mesally facing pocket on the ventral plates. The pocket is shallower and situated closer to the apex than in *Ecnomus* sp. K.

### ***Ecnomus*** sp. K (female)

Figures 36, 37

*Material examined.* East Kalimantan, 1 female, Mahakam River, 250 km W of Samarinda, 10 Mar 1991, C. Yule (NMV); 7 females, Long Hubungan, Mahakam River, 250 km W of Samarinda, 10 Mar 1991, C. Yule (genitalia prep. CT-197 figured, NMV); 3 females, Camp Prampus, Kelian River trib. of Mahakam River, 250 km W of Samarinda, Light trap, 31 Mar 1991, C. Yule (NMV).




Figures 30–37: *Ecnomus* spp., female genitalia. 30, 31, *Ecnomus* sp. H; 30, lateral view; 31, ventral view; 32, 33, *Ecnomus* sp. I; 32, lateral view; 33, ventral view; 34, 35, *Ecnomus* sp. J; 34, lateral view; 35, ventral view; 36, 37, *Ecnomus* sp. K; 36, lateral view; 37, ventral view. All scale lines 0.1mm.

*Description.* Female. Wings fawn to pale brown with paler irrorations, venation characteristic of genus except fork 1 absent on anterior wing. Ventral plates with length about twice width, subrectangular with small apical projections and mesally facing pocket near meso-basal angle (Figs 36, 37).

Length of forewing: female 3.5–3.8 mm.

*Distribution.* East Kalimantan (Indonesia).

*Remarks. Ecnomus* sp. K females are similar to *Ecnomus* sp. J in having mesally facing pockets on the ventral plates. Cartwright (1990) reported that a group of Australian species have laterally facing pockets. Although *Ecnomus* sp. K has aberrant wing venation it cannot be positively associated with either *Ecnomus retusus* or *E. gapit.*

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